SOCIAL ORGANIZATION AND SPATIAL RELATIONSHIPS IN COASTAL RIVER OTTERS: ASSESSING FORM AND FUNCTION OF SOCIAL GROUPS, SEX-BIASED DISPERSAL, AND GENE FLOW

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SOCIAL ORGANIZATION AND SPATIAL RELATIONSHIPS IN COASTAL RIVER OTTERS: ASSESSING FORM AND FUNCTION OF SOCIAL GROUPS, SEX-BIASED DISPERSAL, AND GENE FLOW

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ABSTRACT

River otters (*Lontra canadensis*) inhabiting marine environments are top-level predators foraging in the nearshore ecosystem and recently have been recognized as indicators of environmental health. Otters were extirpated from much of their historic distribution because of exposure to pollution and urbanization, resulting in expansive reintroduction programs that continue today. Without an understanding of the influence of factors such as social structure, mating system, or sex-biased dispersal on genetic variation and gene flow among populations, effects of local extirpation and the potential for natural recolonization (i.e., the need for reintroductions) cannot be determined. The objective of this study was to assess social organization and evaluate the importance of factors such as prey availability and kinship on formation of social groups and dispersal of individuals. Fifty-five otters were radio-tracked in three study areas in Prince William Sound, Alaska, from 1996 to 1999, to determine social organization and dispersal rates. Data from 111 individual otters (seven study areas) were obtained to assess relatedness and gene flow (with microsatellite DNA) and diet (with stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$). DNA analysis indicated that kinship had no effect on social organization or spatial relationships among otters. Analyses of diet and home-range size indicated that social groups may be formed to facilitate cooperative foraging, enabling social otters to obtain a better-quality diet more efficiently (i.e., social otters had diets higher in schooling pelagic fishes and had smaller home ranges, compared to nonsocial otters). Male otters were more social than females, but reproductive constraints likely limited opportunities for sociality among females. Both telemetry and genetic data indicated that

male and female otters had an equal, low probability of natal dispersal and male otters also exhibited breeding dispersal resulting in gene flow to nearby populations. Genetic data indicated distances for natal dispersal were bimodal; most males and some females settled nearby (within 16-30 km), but some females dispersed 60-90 km. Despite lack of geographic barriers to dispersal in a marine system, dispersal distances were relatively short, indicating that extirpation of local populations would be difficult to correct via natural recolonization unless viable otter populations were available nearby.

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INTRODUCTION

The evolution of sociality has long fascinated scientists because of the evolutionary consequences of group living. Two main hypotheses have been advanced: avoidance of predators, and successful acquisition of resources (Alexander, 1974; Gittleman, 1989; Wrangham and Rubenstein, 1986), and such hypotheses are usually assessed in terms of costs versus benefits. Explanations for sociality, based solely upon patterns of social grouping without respect to gender, presume that ecological pressures affect both genders equally (Wrangham and Rubenstein, 1986). Ecological and behavioral constraints affect the sexes differently, mainly because of dissimilarity in reproductive strategies (Bleich et al., 1997). Thus, to understand the evolution of social organization, social relationships and reproductive status of individuals should be considered independently for each gender (Wrangham and Rubenstein, 1986).

River otters inhabiting marine environments show considerable plasticity in social organization. Some otters remain solitary, whereas others occur in large social groups (Blundell et al. *in press a*; Rock et al. 1994; Testa et al. 1994). Because of the shy nature of these mustelids, little is known of their social organization beyond what is gleaned from rare behavioral observations.

The first chapter of my dissertation investigates the form and function of social groups among coastal river otters and explores gender differences in sociality, while testing hypotheses related to avoidance of predation and acquisition of prey. Radio-telemetry data from numerous individuals ($n = 55$) residing in three study areas, allowed for a determination of social organization that was not biased by behavioral observations

of only a few individuals, or events occurring at a single site that may not be representative of sociality for coastal river otters. Additionally, data previously available on food habits for coastal river otters were based upon prey remains in feces (Larsen 1984; Bowyer et al., 1995), which did not permit an evaluation of diets of individuals. The novel approach of combining stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of diets of individual otters and telemetry data, which determined the extent of sociality for those individuals, allowed for the first assessment of how sociality is related to acquisition of food in river otters.

The next two chapters represent the first exploration of form and function of sociality in river otters using genetic data to investigate the link between behavioral ecology and population genetics. In many social animals, obtaining positive identification of individuals and close behavioral observations with which to examine hypotheses pertaining to group associations has been difficult (Hughes 1998). Use of molecular methods (microsatellite DNA) to estimate group structure and genetic relatedness in combination with data on social organization (telemetry data) allow for a critical evaluation of behavioral and ecological interactions that may influence group formation (Hughes 1998, Gompper and Wayne 1996). Integration of molecular data permitted substantiation or rejection of hypotheses regarding social and mating systems that were previously derived solely from behavioral observations (Gompper and Wayne 1996), and afforded the opportunity to challenge existing paradigms and develop new hypotheses (Hughes 1998).

Accordingly, the second chapter examines the role of kinship and sexual selection in defining social structure among coastal river otters. Gregariousness among male river otters raised the question of whether kin selection offered benefits to males. If kin selection operated in this system, otters would be more likely to interact with related individuals, and association with kin might afford some reproductive benefits. In contrast, costs associated with group living may include intraspecific competition for resources or reproductive opportunities (Alexander 1974, Wrangham and Rubenstein 1986). The alternative, but not necessarily mutually exclusive hypothesis explored in chapter two, is that sexual selection for secondary sexual (i.e., morphological) characteristics might influence social organization and reproductive success in male otters.

The final chapter explores how gender differences in sociality and spatial relationships influences dispersal and gene flow. These data, obtained in coastal habitats in a remote wilderness environment without terrestrial or anthropogenic barriers to dispersal (e.g., habitat fragmentation or urbanization), may serve as baseline data for predicting dispersal of river otters under optimal conditions. Such data may be incorporated into predictive models useful for estimating the likelihood of natural recolonization from nearby populations in the event of local extirpation, thereby assessing the need for reintroductions. These data may also be useful for modeling or monitoring current reintroduction projects for otters, or when future translocation projects for river otters are considered.

These data were collected in Prince William Sound, Alaska, 6-8 years after the *Exxon Valdez* oil spill, concurrent with a study assessing whether river otters continued to be influenced by chronic effects from the spill. That study, comparing otters residing in previously oiled and nonoiled areas of the Sound, indicated that although river otters may still be exposed to low levels of crude oil, the effects of that exposure were no longer sufficient to cause obvious injury (Bowyer et al. *in review*). Accordingly, in 1999, the *Exxon Valdez* Oil Spill Trustees Council officially removed river otters from the list of injured species. Similarly, my dissertation research noted no difference in likelihood of dispersal or distances dispersed between otters residing in previously oiled and nonoiled areas, indicating that population dynamics are similar among study sites, regardless of historical exposure of those areas to oil contamination.

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CHAPTER 1

Sociality in river otters: cooperative foraging or reproductive strategies?[1]

We evaluated factors influencing social organization in coastal river otters (*Lontra canadensis*) to test two hypotheses: group formation was an anti-predation strategy, or alternatively was related to cooperative foraging. Data on group size, group composition, and sociality, were obtained through radiotracking 55 otters in Prince William Sound, Alaska, from 1996 through 1998. For males, larger groups occurred after the mating season and concurrent with availability of schooling pelagic fishes and potentially lower risk of predation. Stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis revealed that otters social in >10% of their locations had diets significantly higher in rapidly swimming pelagic fishes than did less social otters, regardless of gender. In addition, otters that were social >50% of the time had smaller home ranges than did less social otters, and asocial otters had the largest home ranges -- an observation consistent with increased foraging efficiency through cooperative foraging. Discounting associations of females with young of the year, approximately 47% of females and only 24% of males were asocial. Among social otters, males were social in 46% of their locations, and 63% of that time occurred in all-male groups. Females were only social in 26% of locations and were in mixed-sex groups 78% of that time. We hypothesize that the time-consuming task of raising offspring prevents females from joining foraging groups. When not raising young,

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[1] G. M. Blundell, M. Ben-David, and R. T. Bowyer. In Press. Sociality in river otters: cooperative foraging or reproductive strategies? Behavioral Ecology.

however, females join males to cooperatively forage for better-quality prey (pelagic fishes), which would be more difficult to acquire as a solitary forager. *Key words*: Alaska, *Lontra canadensis*, predation risk, sexual dietary partitioning, sexual dimorphism, schooling fishes, social organization, stable isotopes.

INTRODUCTION

Sociality and group formation (beyond that of a family unit), usually are assessed in terms of costs and benefits (Alcock, 1993; Mangel, 1990). Avoidance of predators and successful acquisition of food have been proposed as two main hypotheses for group formation (Alexander, 1974; Gittleman, 1989; Wrangham and Rubenstein, 1986). Explanations for sociality, which are based solely upon patterns of social grouping without respect to gender, presume that ecological pressures affect both genders equally (Wrangham and Rubenstein, 1986). Ecological and behavioral constraints affect the sexes differently, however, because of dissimilarity in reproductive strategies (Bleich et al., 1997). Thus, to understand the evolution of social organization, social relationships and reproductive status of individuals should be considered independently for each gender (Wrangham and Rubenstein, 1986).

Carnivora tend toward solitary behavior with aggregates occurring outside of mating season in only 10-15% of species (Gittleman, 1989). Mustelids are among the least social carnivores (Gittleman, 1989), but considerable variation occurs among Lutrinae. Otter behavior ranges from solitary in Eurasian otters (*Lutra lutra*) inhabiting marine environments (Kruuk and Moorhouse, 1991), to monogamous pairs in marine otters (*Lontra felina*) in Chile (Ostfeld et al., 1989), to "family parties" (Proctor,

1963:101) in spotted-necked otters (*Lutra maculicollis*). Family groups with solitary males were observed in North American river otters (*Lontra canadensis*) in a freshwater system (Melquist and Hornocker, 1983). Gregariousness has been reported for male Cape clawless otters (*Aonyx capensis*; Arden-Clarke 1986), and giant otters (*Pteronura brasiliensis*) occur in mixed-gender groups (Duplaix, 1980).

Relatively little is known about the social organization of *L. canadensis* in marine environments. Coastal river otters in Prince William Sound (PWS), Alaska, USA, exhibit high variability in social organization. Recent studies documented the occurrence of solitary individuals (Blundell et al., 2000), concurrent with the existence of large groups of up to 18 individuals (Blundell et al., 2000; Rock et al., 1994; Testa et al., 1994). In addition, scent marking at communal latrines (Ben-David et al. 1998; Bowyer et al., 1995; Testa et al., 1994), and helping behavior have been reported in this population (Rock et al., 1994). Herein, we explore hypotheses forwarded to explain sociality and examine their efficacy in elucidating the function of group formation in coastal *L. canadensis*.

Formation of large groups in river otters may result in a collective increase in vigilance for predators (Rasa, 1986) and lower the probability of being selected as prey (*sensu* Hamilton, 1971). Thus, under conditions of high predation risk when food resources are abundant, both sexes should exhibit high degrees of sociality. Nonetheless, gregariousness may increase the ability of a predator to detect prey (Alcock, 1993; Gittleman, 1989; Rubenstein, 1978), as well as increase the risk of infanticide for young in mixed-gender groups (Alcock, 1993; Packer and Pusey, 1984; Kruuk H, personal communication, for infanticide in *L. lutra*). Under such conditions, we predict that group

composition and the degree of sociality will differ between the genders. Furthermore, if risk of predation remains relatively constant year-round and group formation is an anti-predation strategy, we predict that group size in coastal river otters will not vary with season.

In PWS, river otters have access to two major types of prey: schooling pelagic fishes, which are available seasonally (Ben-David et al., 1998; Brown et al., 1999; Dean et al., 2000) and have high energy density, and intertidal-demersal organisms that are easier to capture but are lower in quality (Anthony et al., 2000; Bowyer et al., 1994). Formation of groups and cooperative foraging (or "by-product mutualism"; Connor, 1986) among aquatic predators result in increases in individual capture success of schooling fishes (Baird and Dill, 1995, Götmark et al., 1986; Norris and Schilt, 1988). Under such conditions, we predict that more social otters would have diets higher in better-quality pelagic fishes, compared with otters that exhibit low levels of sociality. Further, we hypothesize that if sociality enhances foraging success, group size will change seasonally, tracking the seasonal changes in availability of schooling pelagic fishes in the nearshore environment. In addition, increased foraging efficiency as a result of cooperative foraging likely will be negatively related to home range or territory size (Herrman, 1994; Woodroffe and MacDonald, 1993). Thus, we predict that otters exhibiting higher degrees of sociality would require less space in which to meet their energetic demands and would have smaller home ranges.

Otters inhabiting marine environments occupy a long, narrow stretch at the marine-terrestrial interface (Arden-Clarke, 1986; Blundell et al., 2001; Bowyer et al.,

1995; Kruuk and Moorhouse, 1991). Although such a range shape may be difficult to defend due to a high perimeter to area ratio (Kruuk, 1989), formation of large groups may facilitate the defense of group territories. Under such conditions, we predict that social otters would have larger home ranges compared with less social animals.

Finally, hypotheses for explaining sociality in coastal river otters can be derived from differential ecological constraints and reproductive strategies of genders. In diving mammals, structural size and muscle mass likely influence swimming ability (Fish, 1994). Therefore, sexual dimorphism (Moors, 1980) may afford larger male otters superior swimming abilities. Under such conditions, we hypothesize that diets of males would be composed of more pelagic fishes than would those of females, representing higher efficiency at capturing rapidly swimming schooling fishes.

Differences between genders in reproductive strategies (Wrangham and Rubenstein, 1986) also may influence degree of sociality in river otters. Male-male competition for reproductive opportunities likely would be the main constraint on sociality and cooperative foraging for male otters (Le Boeuf and Reiter, 1988), because *L. canadensis* males do not participate in rearing of offspring (Melquist and Hornocker, 1983; Rock et al., 1994). Nonetheless, the short mating season in Alaska (lasting approximately 1 month; Blundell GM, personal observation; Woolington, 1984), will only influence sociality in males for a brief period. In contrast, females spend much of the year raising young and are spatially restricted in their movements during that time (Noll, 1988), limiting their opportunities for cooperative foraging. Thus, we hypothesize that males will spend more time in social groups than females, and male

group size will decrease prior to and during mating season. Alternatively, formation of male coalitions may increase male reproductive success (Packer et al., 1991; Witt et al., 1981). Under such conditions, we would expect group size for males to increase or remain large during the mating season.

Many of the hypotheses we discuss are not mutually exclusive and often result in similar predictions, making critical tests difficult. Therefore, we use a weight of evidence approach in evaluating the importance of different ecological factors in influencing sociality in coastal river otters.

METHODS

Study Areas

Our study areas are located in western Prince William Sound, Alaska, USA, spanning an area of approximately 4,800 km^2. Detailed descriptions of the study areas and a map are provided in Ben-David et al. (1998) and Bowyer et al. (1995). Fieldwork was conducted in 1996 and 1997 in Jackpot, Ewan, and Paddy bays along Dangerous Passage (60° 20'N, 148° 10'W), and in Herring Bay and surrounding areas on northern Knight Island (60° 23'N, 147° 40'W). In 1998, our study areas included Herring Bay, Eleanor Island (60° 32'N, 147° 37'W), Esther Passage (60° 53'N, 147° 55'W), Unakwik Inlet (60° 55'N, 147° 30'W), Wells Bay (60° 55'N, 147 ° 20'W), and Naked Island (60° 40'N, 147° 25'W).

Live capture of otters

We live-captured 111 individual river otters from May through July in 1996 and 1997, and from mid-April through May in 1998, with No. 11 Sleepy Creek® double-jaw

leg-hold traps or with Hancock traps (Blundell et al., 1999). A subset of otters (n = 55) from three of our study areas (Dangerous Passage, northern Knight Island, and Eleanor Island), were equipped with radiotransmitters (Blundell et al., 2000). Further details on capture and handling are provided in Blundell et al. (1999). All methods used in this research were approved by the Institutional Animal Care and Use Committee at UAF and adhere to the ABS/ASAB guidelines for ethical treatment of animals.

Radiotelemetry and sociality

We obtained information on sociality in otters using radiotelemetry. Radiotracking was conducted either from a boat (in 1996), or from a small fixed-wing aircraft (1997-1998). Tracking by boat occurred 2-3 times/week in July and August. Aerial tracking occurred approximately every 4 days from mid-April through mid-June to monitor shifts in activity around the mating season. Thereafter, tracking was conducted weekly until September and every 2-3 weeks during winter. In 1996, we radiotracked 12 otters in marine systems ($\bar{x}$ = 19.7 locations per otter, SE = 1.4), 18 otters in 1997 ($\bar{x}$ = 25.5 locations, SE = 1.0), and 34 otters in 1998 ($\bar{x}$ = 25.4 locations, SE = 1.4). Radiotracking of individual otters ranged from 41 to 994 days ($\bar{x}$ = 416, SE = 37). Further details regarding collection of telemetry data are provided in Blundell et al. (2000; 2001).

Once a telemetered otter was located, GPS data were obtained and radio frequencies of all other otters were scanned to determine whether other individuals were present in the same location. During visual observations, presence of unmarked animals was determined. Our assessment of sociality in female otters does not reflect the

association of a female with her offspring of that year. Group association as determined by the pilot was ground truthed twice and verified as accurate by an independent observer.

Our estimates of sociality likely represent underestimates because visual observations were infrequent (83 of 1,972 locations or 4.2%) and telemetered otters may have been traveling with unmarked animals. When otters were sighted, however, approximately two-thirds of those observations revealed that radiotagged otters were not traveling with unmarked individuals, usually confirming the incidence of solitary individuals. Therefore, our telemetry observations likely represent a reasonable estimate of sociality (minimum group size) in river otters.

Diet and morphometrics

Fur samples (under fur and guard hair) were collected from otters for diet analysis with stable isotope ratios (Ben-David et al., 1998). River otters fully shed and replaced under fur from May through August, and guard hair from August to November (Ben-David M, personal observation; Ben-David et al., 2000). Thus, stable isotope analysis of those two types of hair allowed for an assessment of seasonal diets. Details on protocols for stable isotope analysis are provided in Ben-David et al. (1998).

Stable isotope values for fish tissues collected in PWS were obtained from companion studies by Ben-David et al. (1998), Hirons A (Institute of Marine Sciences, University of Alaska Fairbanks), and Kline TC (Prince William Sound Science Center, Cordova, Alaska) with identical procedures.

We collected morphometric data from anesthetized otters including: body mass (nearest 0.1 kg); and body length, tail length, and total length (nearest 1 mm). In 1997-1998, we also measured interdigital spread of the right hind foot to the nearest 0.1 mm. Age of otters (pup, young adult, adult, and old adult) was estimated based on body size, and tooth wear and staining.

Data analyses

Group size

We determined minimum group size for otters based upon telemetry and visual observations. For each otter, the total number (telemetered + unmarked, if visual observation) of otters in the group was recorded for each observation. To test whether group size varied with the availability of schooling prey for each gender, we used a two-way analysis of variance (ANOVA; Zar, 1996), with month and gender as main effects, age as a random factor, and average group size as the dependent variable. We followed with post-hoc Scheffe multiple comparisons among months and ages. To explore the relation between changes in group size of otters relative to the timing of availability of pelagic fishes, we adapted data from Brown et al. (1999; personal communication E. Brown - ADF&G unpublished data) and Groot and Margolis (1991).

Sociality

Among the three intensive study areas (Dangerous Passage, northern Knight Island, and Eleanor Island; Figure 1.1), one area (Dangerous Passage) has an extensive freshwater system immediately adjacent to the marine system. Consequently, otters inhabiting that area had access to freshwater fishes and habitats, as well as numerous

seasonal runs of spawning salmon (*Oncorhynchus sp.*; Blundell et al., 2000), which were not available with similar abundance in the other study areas. To control for differential effects of prey availability on sociality and home-range size among areas, we used data only from otters that used the marine system >70% of the time. We analyzed our telemetry data in yearly increments to include one reproductive cycle and seasonal fluctuations in availability of prey. We used each year of telemetry data for each otter as an independent sample. Accordingly, 55 otters sampled across 3 years yielded a total of 64 instances that were used for our analyses of sociality. We corrected for pseudoreplication by blocking by otter in all analyses concerning degree of sociality.

For each otter, we calculated proportion of social locations (occurrence with at least one additional otter). We tested for significant differences in sociality between genders with a chi-square analysis (Conover, 1980). We assigned otters to one of four categories: none (0% of the annual locations were social); low (≤10% social locations), moderate (11-50% social), and high (>50% social). For social otters, we explored gender differences in the proportion of social locations with one-way ANOVA. We also conducted a chi-square analysis to compare, by gender, the proportion of social otters that occurred in mixed-sex groups.

Diet

To determine whether isotopic signatures of intertidal-demersal fishes, pelagic fishes, and freshwater fishes differed significantly, we employed the K nearest-neighbor randomization test (Rosing et al., 1998). We used a two-way multivariate analysis of

variance (MANOVA; Johnson and Wichern, 1988) with $\delta^{13}C$ and $\delta^{15}N$ as dependent variables to compare diets of otters between season and gender.

Our sample size was smaller when stable isotopes were paired with telemetry data for each individual, because only the year of spatial data that most closely corresponded to the year of dietary data was used. Consequently, we considered only two categories of sociality (low ≤10%, and high >10% social locations) for comparison of diet and sociality. We used one-way ANOVA with degree of sociality and gender as independent variables, otter as a random factor, and $\delta^{13}C$ as the dependent variable. We excluded $\delta^{15}N$ from this analysis because carbon signatures more clearly distinguish between prey groups in our system. We followed that analysis with a Wilcoxon test to determine whether seasonal changes occurred in diets of otters, for both low and high categories of sociality.

Home-range size and sociality

Home ranges were estimated with fixed-kernel analyses and the reference smoothing parameter (Blundell et al., 2001). We obtained home-range contours for 95% isopleths for each otter in each year with RANGES V (Kenward and Hodder, 1996). Because otters generally confine their movements to the shoreline, we measured the kilometers of shoreline within those home-range contours (Blundell et al., 2001; Sauer et al., 1999) with the Geographic Information System (GIS) ARC/INFO (Redlands, CA, USA).

To test whether more social otters had smaller home ranges, we compared home-range size by category of sociality (none, low, moderate, and high). We used one-way

ANOVA with post-hoc Scheffe multiple comparisons among categories. We conducted the analysis without respect to gender, assuming that within a social group both genders would experience the same conditions.

Morphometrics

To determine the degree of sexual dimorphism in otters, we used MANOVA to compare morphometric measurements between genders and included age as a covariate to control for effects of age on size. We used the ratio of weight to total length to assess overall sexual dimorphism, and also compared body length, tail length, interdigital spread, and body weight between sexes.

RESULTS

Group size

Average minimum group size in all years differed among months for male, but not female otters (Figure 1.1). Changes in group size corresponded to availability of pelagic fishes (Figure 1.1). Groups composed of up to 8 or 9 individuals were sighted from late May until mid-September, whereas groups of >4 individuals were not observed after early September. Group size differed by age class for males ($p = 0.002$, ANOVA), with juveniles occurring singularly or in smaller groups more often than did older animals. Group size did not differ among age classes for females ($p = 0.8$, ANOVA), and the interaction between age class and month was not significant for either sex ($p > 0.5$, ANOVA). In the overall model, month, gender, and age were significantly different ($p < 0.001$, ANOVA); interactions did not differ ($p > 0.24$, ANOVA). Because group size

differed by age class only for juvenile males, and juvenile males were few (6% of 64), we did not consider effects of age in further analyses.

Sociality

Males and females differed significantly in degree of sociality. Only 24.4% of male otters were solitary, compared with 47.4% of females (Figure 1.2). Females occurred primarily in low and moderate categories of sociality, and males occurred most often in moderate and high categories of sociality; this trend was marginally nonsignificant (Figure 1.2). Differences in sociality between genders were highly significant ($p = 0.03$, χ^2 test) when we examined occurrence in low (≤10%) and high (>10%) categories of sociality (males: low = 37.8%, high = 62.2%; females: low = 68.4%, high = 31.6%).

Among social otters, males were gregarious more often (46% ± 4% SE of all locations per year, $n = 34$) than females (26% ± 6% SE, $n = 10$; $p = 0.03$, ANOVA). Additionally, males occurred in mixed-gender groups only 37.5% of the time ($n = 32$), whereas social females were in mixed-gender groups in 77.8% of their locations ($n = 9$; $p = 0.03$; χ^2 test).

Diet – stable isotope analyses

Of all fish sampled, only herring (*Clupea pallasi*) and adult salmon (*Oncorhyncus gorbushcha*), and sand lance (*Ammodytes hexapterus*) and juvenile salmon *Oncorhyncus sp.*) had overlapping isotopic ratios ($p = 0.55$, and 0.76, respectively; K nearest-neighbor). When pooled by groups, intertidal and demersal fishes, pelagic fishes, and freshwater fishes all had significantly different isotopic values ($p < 0.05$; K nearest-

neighbor; Table 1.1). Diets of male and female otters were significantly different during spring and early summer (Figure 1.3a). That difference became more pronounced later in the summer and autumn (Figure 1.3b). During that latter period, more males than females shifted to include pelagic fishes in their diet as indicated by more depleted signatures of both $\delta^{13}C$ and $\delta^{15}N$ (Figure 1.3b). Eleven of 34 females (32%) changed their diet, compared with 43% of 82 males. The overall model of sex by season (hair type) was significant ($p < 0.001$ for $\delta^{13}C$ and $\delta^{15}N$, MANOVA). No difference occurred in $\delta^{13}C$ by season ($p = 0.8$) but $\delta^{15}N$ differed seasonally ($p < 0.001$). Values for each isotope differed between genders ($p < 0.002$), but the interaction between season and sex was not significant for $\delta^{13}C$ or $\delta^{15}N$ ($p > 0.1$).

Analysis of diet, as represented by isotopic ratios of under fur and guard hair, in relation to sociality, revealed that values of $\delta^{13}C$ were significantly different between categories of sociality, but not between genders (overall model $p = 0.02$; sociality $p = 0.02$; gender $p = 0.8$, ANOVA). Significant differences occurred in diet between sociality categories for spring-summer (low sociality average $\delta^{13}C$ – 14.58 ± 0.01 SE, $n = 25$, high sociality average $\delta^{13}C$ – 15.16 ± 0.02 SE, $n = 32$; $p = 0.006$; ANOVA). Similarly, significant differences occurred in summer-autumn (low sociality average $\delta^{13}C$ – 14.55 ± 0.02 SE, $n = 25$, high sociality average $\delta^{13}C$ – 15.35 ± 0.04 SE, $n = 32$; $p = 0.004$; ANOVA), indicating that those animals with lower levels of sociality had diets composed primarily of intertidal and demersal fishes during both seasons, and highly social animals had ^{13}C signatures consistent with an increased pelagic component in the diet. No significant difference in diet existed between seasons within sociality

categories; low sociality ($p = 0.255$; Wilcoxon test) and high sociality ($p = 0.16$; Wilcoxon test).

Sociality and home-range size

Otters that exhibited high sociality had the smallest home ranges (Figure 1.4) and nonsocial otters had the largest home ranges ($p < 0.05$, ANOVA). Intermediate categories of sociality were indistinguishable from each other. Overall, differences in home-range size among sociality categories were marginally nonsignificant ($p = 0.1$).

Morphometrics

Male otters were significantly larger than females (Table 1.2) but dimorphism was not pronounced ($p = 0.04$, overall model MANOVA). The weight-length ratio of male otters was only 10.8% greater than that of females. Males weighed an average of 1.1 kg more than females, but body length did not differ between genders (Table 1.1). Tail length and interdigital spread were significantly larger for males than for females (Table 1.1).

DISCUSSION

Our data support predictions associated with the hypothesis that group formation facilitates cooperative foraging. That group size in males increased between May and October and decreased thereafter, tracking the availability of schooling pelagic fishes in the nearshore environment (Figure 1.1), supported the hypothesis that sociality was a foraging strategy, at least for male otters. Group size among males did not change with availability of herring spawn (Figure 1.1). It is, however, eggs rather than spawning fishes that are primarily targeted by otters during spawning events (Blundell personal

observation) and spawn can be obtained in abundance by solitary otters. Similarly, more social animals had smaller home ranges, suggesting greater efficiency in foraging (Figure 1.4). Male otters have significantly larger home ranges than do females (Blundell et al. 2000) but we did not consider home-range size for each gender independently in our analysis of home-range size and sociality. Our data are strongly male-biased and highly social otters are mostly males (Figure 1.2). Therefore, that home-range size for highly social otters is significantly smaller than that of nonsocial animals (Figure 1.4), which are mostly females (Figure 1.2), indicates that our results are not a function of gender differences in home-range size. That analysis provides strong evidence that sociality affects home-range size and that more social otters require less space in which to meet their energetic needs, potentially via cooperative foraging. A higher incidence of pelagic fishes in diets of more social otters also indicates that social otters may be cooperatively foraging. Indeed, observations in which otters cooperated to drive fish toward shore or toward one another have been reported in freshwater habitats for *L. canadensis* (Sheldon and Toll, 1964; Serfass, 1995) and for *L. perspicillata* (Kruuk et al., 1994). Furthermore, in other species, successful evasion of predation by schools of fishes was inversely proportional to the number of predators in the group (Götmark et al., 1986; Pitcher and Parrish, 1993), thus foraging in groups may be beneficial to river otters.

Sexual dietary partitioning (Figure 1.3) in otters may reflect differential swimming abilities between genders. Sexual dimorphism among river otters was subtle (Table 1.2), but higher body mass may confer superior swimming ability to males. We hypothesize that larger body mass in males is likely a result of greater skeletal muscle mass distributed

along a frame similar in length to that of females. Such structure, together with larger feet, may provide males with greater undulating power and propulsion (Fish, 1994), potentially increasing their swimming speed or efficiency. A school of pelagic fish moves rapidly and erratically as a polarized unit, or sometimes splits into several schools, thereby confusing a solitary predator (Norris and Schilt, 1988). Therefore, sexual dimorphism may not be sufficient to explain sexual dietary partitioning in coastal river otters without the formation of groups.

Norris and Schilt (1988) observed that fishes receiving simultaneous cues from multiple predators were unable to respond with polarized or evasive movements, leading to a decrease in inter-fish distance (Major, 1978) and a greater capture success for individuals foraging in a group, compared with solitary foragers (Götmark et al., 1986; Norris and Schilt, 1988). Rich ephemeral patches of schooling fishes in the nearshore environment in PWS (Brown et al., 1999; Groot and Margolis, 1991) cannot be exploited at a single feeding and fit assumptions of foraging models in which unequal competitors fare equally well (Rita et al., 1996). That male otters exhibited higher sociality than females (Figures 1.1 and 1.2), that female otters joined male groups, and that sociality influenced the consumption of pelagic fishes regardless of gender (Figure 1.3), indicate that sexual dimorphism may not be a critical factor in foraging strategies of otters. Therefore, cooperative foraging by coastal river otters on schooling fishes should result in increased access to better quality prey – a benefit that likely would be afforded to all group members, regardless of gender or swimming ability.

Although the weight of evidence indicates that sociality in coastal river otters may be a foraging strategy, we cannot critically evaluate hypotheses concerning predation. Nonetheless, an increase in group size solely to avoid predation is not likely to have resulted in differential diets between otters with varying degrees of sociality. Increased foraging efficiency and anti-predator strategies might be jointly employed, however, to allow more social otters to forage for pelagic fishes farther offshore, potentially facing greater risk of predation. Blundell et al. (2001) evaluated data collected during intense behavioral observations of river otters conducted in PWS in 1991 (Rock et al. 1994) and reported that otters observed from boats during that study (n = 119 observations) foraged an average of 5.1 m from shore (SE = 0.9, range 1 – 80 m). For those data, there was a negative correlation between group size ($\bar{x}$ = 4.1, SE = 0.2, range 1 to 8 otters; unpublished data) and distance from shore (r = -0.2; unpublished data); thus larger group size among coastal river otters did not appear to promote foraging farther from shore.

We cannot assess predation risk for river otters because of difficulties inherent in observing most predators. Potential predators may include killer whales (*Orcinus orca*), sea lions (*Eumetopias jubatus*), seals (*Phoca vitulina*), salmon sharks (*Lamna ditropis*), terrestrial carnivores (e.g., wolves, *Canis lupus*), and, for young otters, bald eagles (*Haliaeetus leucocephalus*). With the exception of minor predation by wolves (Kohira and Rexstad, 1997), however, no incident of successful predation by other species has been reported for river otters. Information on transient killer whales, which prey on marine mammals (Baird and Dill, 1995), indicates there is little change in their occurrence by season in PWS (Saulitis et al., 2000). Thus, existing evidence suggests that

predation pressure for river otters is not likely to vary seasonally. If at all, we would expect predation pressure on river otters to increase in winter. Given the absence of forage fish and salmon from PWS between November and May (Figure 1.1), fish predators such as sea lions (Merrick et al., 1997) and seals (Pitcher, 1980) likely would switch to alternative prey during that time (Taylor, 1984). Our results indicate that group size for male river otters significantly increased between May and October (Figure 1.1), which does not correspond to a known increase in predation risk in the sound.

Predation risk also may impose some limitations on sociality for reproductive females. In ungulates, females with young sometimes choose a lower-quality habitat and thus a lower-quality diet to reduce predation risk (Bleich et al., 1997). Similarly, avoidance of social groups may limit opportunities for cooperative foraging in female river otters with young, resulting in a lower-quality diet for females. The relation between sociality as an anti-predation strategy and its consequences for male and female river otters warrants further study.

Our data demonstrated that male otters were generally more social than females (Figures 1.1 and 1.2). In Alaska, the mating season for river otters occurs in May (Blundell GM, personal observation; Noll, 1988; Woolington, 1984) prior to the arrival of large numbers of pelagic fishes (Figure 1.1). Data on testicle width, testosterone secretion, and increased aggression between individuals in captive male otters (Ben-David M, Unpublished data) indicated that timing of male-male competition for mates occurs in late-March to late-May, prior to the increase in pelagic fishes (Figure 1.1). Thus, during the period when aggression (i.e., costs of sociality) would be escalated

between males, benefits of sociality (cooperative foraging) are limited and highly nutritious herring spawn are available (Figure 1.1), which does not require cooperation among otters to obtain.

Although little is known about the mating system for coastal river otters, our data indicate that sociality in males cannot be attributed to male mating coalitions. Group size significantly declined prior to and during mating season, providing no support for that hypothesis. Conversely, that observation supports the hypothesis that males may compete for reproductive opportunities. Why some males appear to remain solitary year-round, however, is unclear and merits further investigation.

Reproductive females may experience greater constraints on sociality than males, because they are restricted in movements for a large part of the year (Noll, 1988). River otter neonates are kept in natal dens for approximately 8 weeks (Noll, 1988). This is followed by several months of post emergence period (Melquist and Hornocker, 1983) in which the movements of a female remain restricted compared with the size of her pre-denning home range (Noll, 1988). Therefore, between parturition (early May; Noll, 1988), and October, reproductive females might have difficulty in locating a group of cooperatively foraging otters. Consequently, options for cooperative foraging while raising offspring likely would be limited, resulting in the sexual dietary segregation we observed (Figure 1.3).

Although we were unable to directly evaluate the role of risk of predation or infanticide, our data provide considerable evidence that cooperative foraging is a key factor influencing social organization of coastal river otters. We suggest that the higher

incidence of pelagic fishes in diets of male otters is not a result of sexual dimorphism and superior swimming ability; rather, it is a benefit of sociality. Males have few constraints on sociality. Sociality, however, would be most beneficial when rich, ephemeral patches of schooling fishes are available as indicated by the seasonal changes in group sizes of males. Furthermore, we suggest that otters may switch strategies from social to nonsocial, depending upon the time of year, prey availability, their gender, and their reproductive status. Reproductively active females likely are prevented from social interactions with groups during most of the year while undertaking the time-consuming task of raising offspring. During years in which a female is not raising offspring, however, her best strategy is to join a group to take advantage of the benefits of cooperative foraging and the associated increased access to a better quality diet that would be difficult to obtain as a solitary forager.

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Table 1.1. Values of stable isotope ratios for fish tissues collected in Prince William Sound, Alaska. Data obtained from companion studies (Ben-David et al., 1998; Hirons A, Institute of Marine Sciences, University of Alaska Fairbanks; Kline TC, Prince William Sound Science Center, Cordova, Alaska). Pelagic fishes are defined as schooling fishes occurring seasonally in the nearshore environment that have a pelagic or open-ocean phase in their life cycle.

Group	Species		*n*	$\delta^{13}C$	SE	$\delta^{15}N$	SE
Pelagic	Capelin	*Mallotus villosus*	19	-22.7	0.4	11.9	0.4
	Pacific sand lance	*Ammodytes hexapterus*	22	-19.5	0.06	11.1	0.08
	Pacific herring	*Clupea pallasi*	15	-20.2	0.2	12.5	0.2
	Salmon (Juvenile)	*Oncorhynchus sp.*	10	-19.8	0.4	11.3	0.3
	Salmon	*Oncorhynchus gorbuscha*	43	-20.1	0.2	12.6	0.2
Intertidal-demersal	Cod	*Gadus macrocephalus* and *Theragra chalcogramma*	6	-17.5	0.14	12.1	0.16
	Greenling	*Hexagrammos decagrammus*	61	-17.5	0.09	14.5	0.09
	Gunnel	*Pholis laeta*	44	-16.1	0.1	12.6	0.03
	Rockfish	*Sebastes* sp.	2	-14.6	0.5	16.3	0.7
	Pricklebacks and	*Anoplarchus purpurescens, Stichaeus punctatus, Lumpenus maculatus,*	10	-16.4	0.2	13.7	0.1
	Ronquil	*Xiphister atropurpureus, X. muscosus,* and *Bathymaster signatus,*					

Table 1.1. cont.

Group	Species		*n*	$\delta^{13}C$	SE	$\delta^{15}N$	SE
	Intertidal sculpins	*Oligocottus maculosus* and *Icelinus borealis*	12	-17.1	0.2	15.1	0.16
Freshwater	Coast range sculpin	*Cottus aleuticus*	9	-23.5	0.36	13.5	0.27
	Dolly varden	*Salvelinus malma*	11	-25.6	0.35	11.5	0.25
	Sticklebacks	*Gasterosteus aculeatus*	14	-29.3	0.6	10.0	0.30

Table 1.2. Morphometric measurements for female and male river otters captured in western Prince William Sound, Alaska, USA, from 1996-1998.

Morphological Characteristic	Females			Males			
	n	$\bar{x}$	**SE**	***n***	$\bar{x}$	**SE**	***p*-value**
Weight/Total Length	35	6.4	0.14	81	7.3	0.1	<0.001
Weight (kg)	35	8.1	0.2	81	9.2	0.2	<0.001
Body Length (mm)	35	774	7.1	81	773	10.2	0.99
Tail Length (mm)	35	472	7.0	81	500	10.5	0.03
Interdigital Spread (mm)	21	91.3	1.4	54	98.3	0.8	<0.001

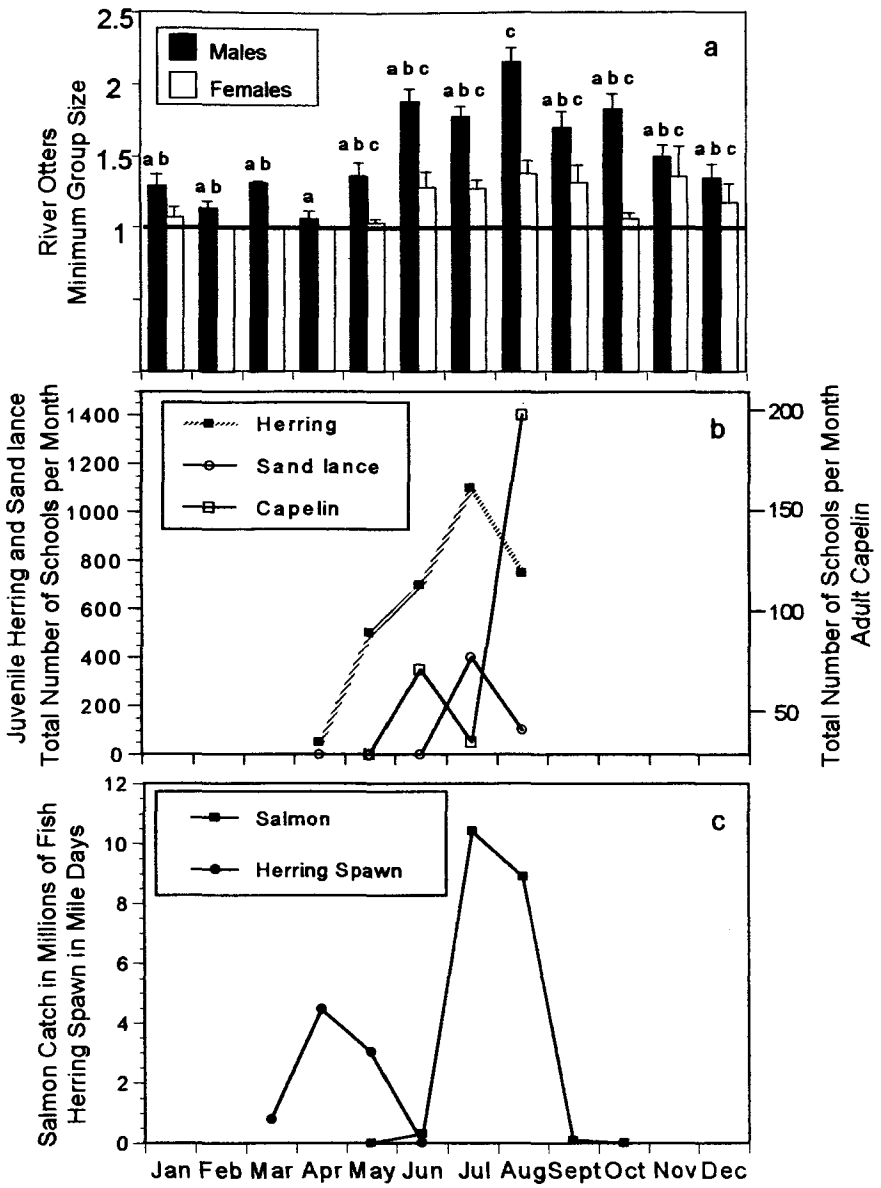

Figure 1.1 – Mean minimum size of groups for river otters inhabiting Prince William Sound, Alaska from 1996 to 1998 (top) in relation to availability of surface schools of pelagic fishes in the nearshore environment (middle; adapted from Brown et al., 1999), and the period of salmon availability (bottom) in southcentral Alaska and Prince William Sound (adapted from Groot and Margolis, 1991) and herring spawn measured in miles of aerial transects (ADF&G unpublished data, E. Brown personal communication). Average minimum group size differed among months for male otters (overall model and month $p < 0.001$ ANOVA), but not for females (overall model $p = 0.13$, month $p = 0.18$ ANOVA). Horizontal line represents minimum possible group size (1 animal). Different letters above columns indicate significant differences among months for male otters at $\alpha = 0.05$; similarity within month clusters for males was a: $p = 0.11$; b: $p = 0.11$; c: $p = 0.054$ (ANOVA, Scheffe multiple comparisons).

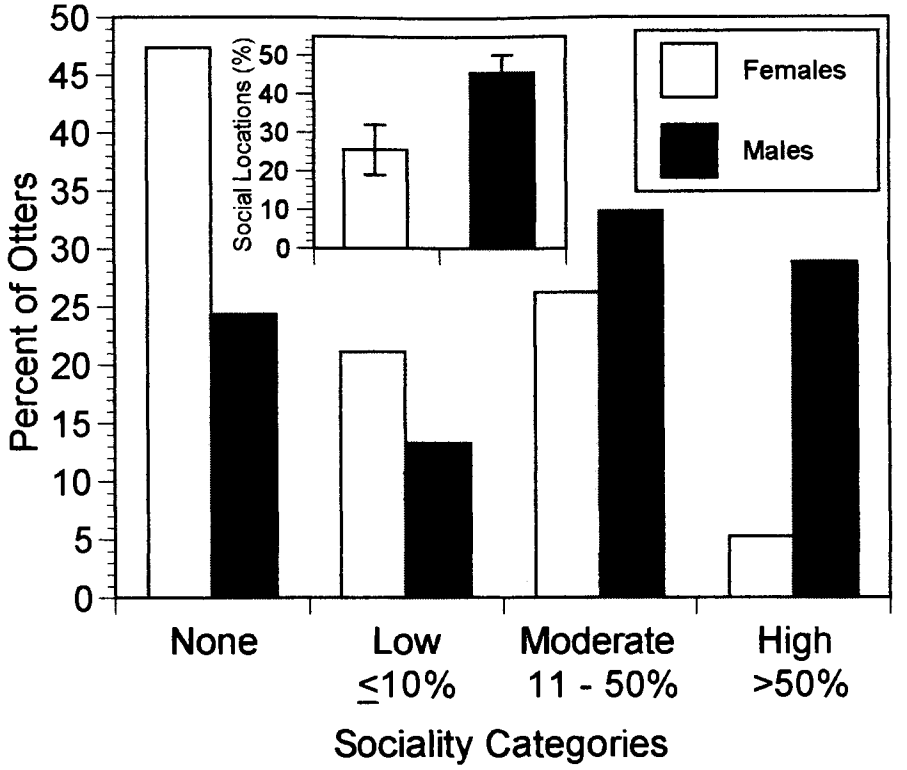

Figure 1.2 - Degree of sociality (proportion of social locations for each otter in a given year) in male and female coastal river otters in Prince William Sound, Alaska, from 1996-1998. Inset: A comparison between genders of proportion of locations that are social each year, excluding nonsocial otters. Males were significantly more social than females ($p = 0.03$ ANOVA).

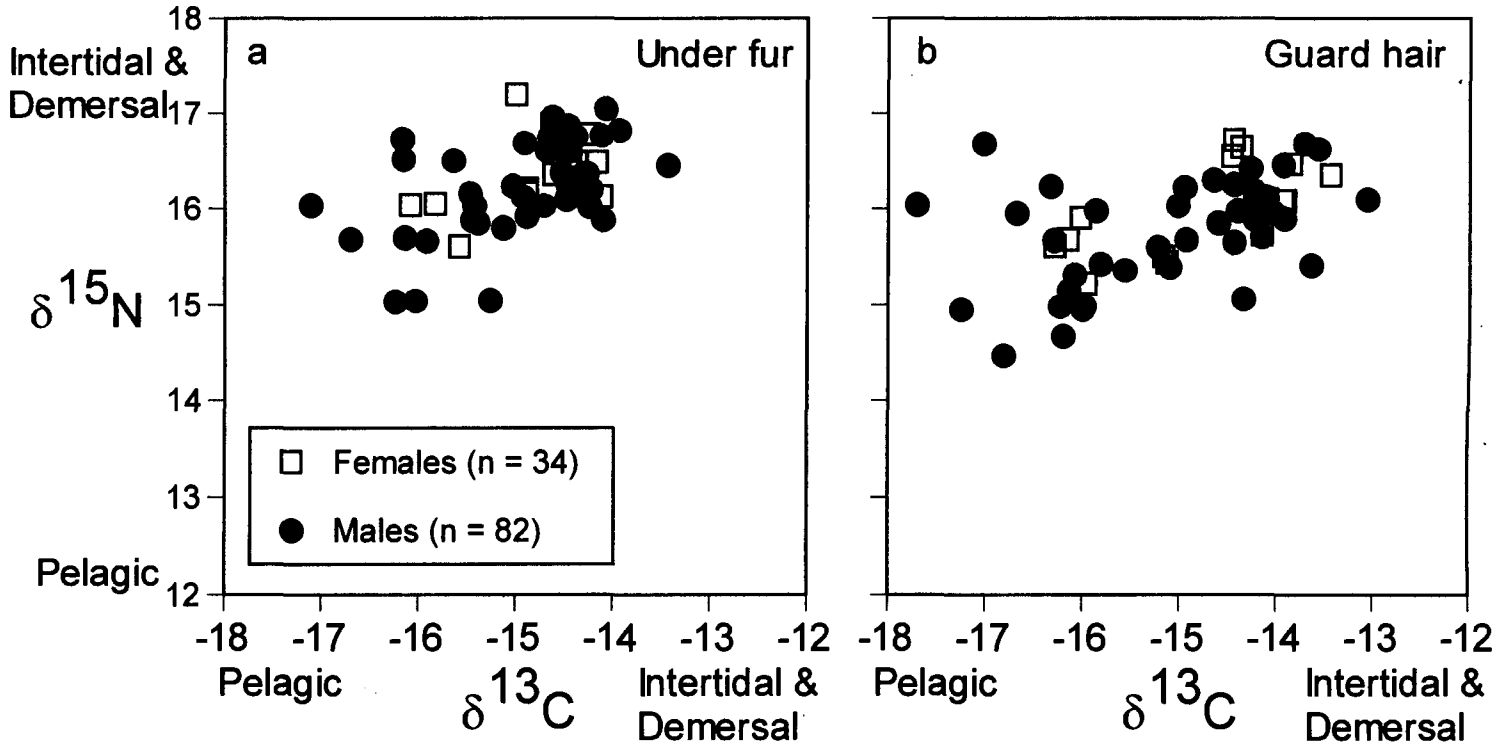

Figure 1.3 – Stable isotope ratios indicating seasonal diets of male and female river otters in Prince William Sound, Alaska. Stable isotope signatures of hair samples represent the diet consumed at the time of hair replacement. Although diets of male and female otters were significantly different during the spring and early summer season (a; Under fur: overall model $p = 0.026$; MANOVA, $\delta^{13}C - p = 0.007$, $\delta^{15}N - p = 0.228$), this difference became more pronounced later in the summer and fall (b; Guard hair: overall model $p = 0.004$; MANOVA, $\delta^{13}C - p = 0.004$, $\delta^{15}N - p = 0.004$).

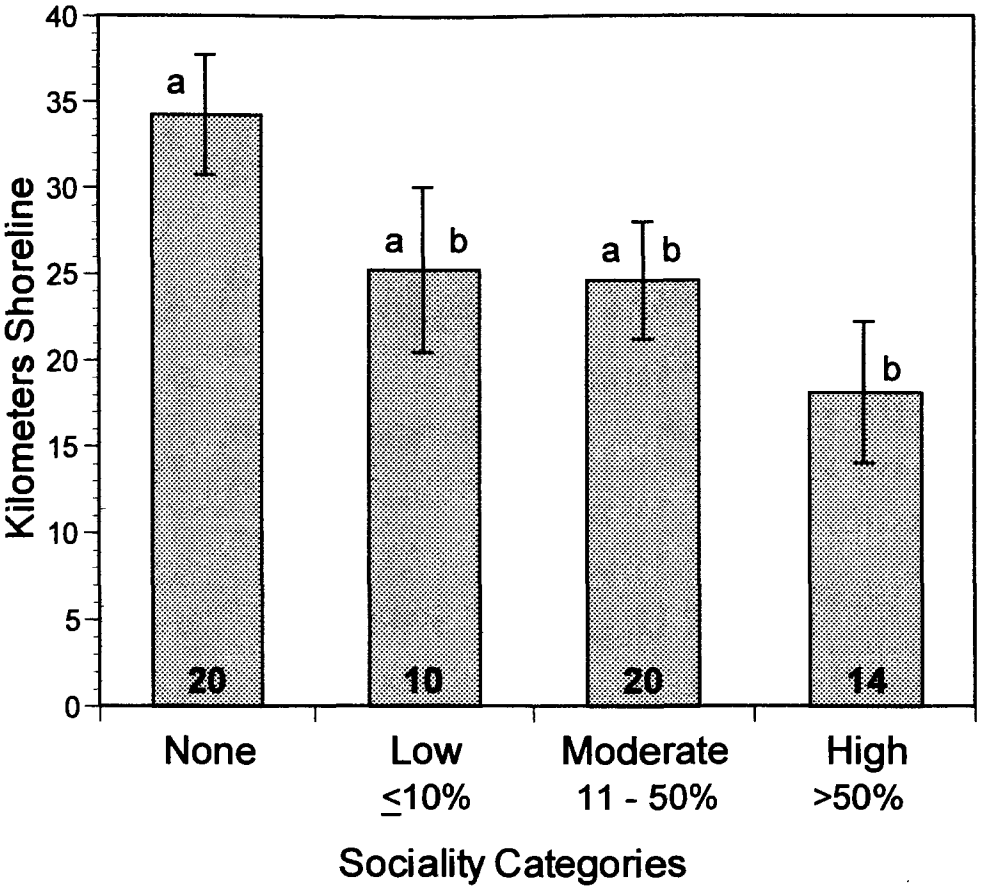

Figure1.4 – Shoreline length (km) measured within 95% contours of home-ranges for the different sociality categories in coastal river otters from Prince William Sound, Alaska. Non social otters had significantly larger home ranges than did highly social animals ($p < 0.05$; ANOVA). Differences between asocial and intermediate categories of sociality and between intermediate and high sociality categories were marginally nonsignificant (a: $p = 0.1$ and b: $p = 0.06$, respectively; ANOVA, Scheffe multiple comparisons).

CHAPTER 2

Formation of social groups in coastal river otters: kinship and reproductive success[2]

SUMMARY

1. Previous studies of coastal river otters (*Lontra canadensis* Schreber 1776) documented atypical social organisation for mammals. Social groups (≤18 otters) were composed largely of males, but some males remained solitary year-round and most females were solitary.
2. Kin selection has been invoked to explain social organisation in *Panthera leo*, another carnivore exhibiting high sociality among males. Gregariousness among male river otters raised the question of whether association with kin offered benefits to male otters similar to those experienced by male African lions.
3. In this study, we used microsatellite DNA, morphometrics, and behavioural data to examine the role of kinship and sexual selection in defining social structure in river otters inhabiting marine environments in Prince William Sound, Alaska, USA. We hypothesised that if kin selection operated in this system, otters would be more likely to interact with related individuals. Alternatively, we hypothesised that sexual selection for morphological characteristics might influence social organisation and reproductive success in male otters. We predicted that larger males would have more

[2] G. M. Blundell, M. Ben-David, P. Groves, R. T. Bowyer, and E. Geffen. In Review. Formation of social groups in coastal river otters: kinship and reproductive success. Journal of Animal Ecology.

offspring, and if sociality conferred a size advantage, larger males would be social. If, however, sociality resulted in reduced mating opportunities (i.e., increased competition) and large size was advantageous, solitary males would be larger and sire more offspring.

4. We noted no association between kinship of otters and any measure of sociality or spatial proximity. Social groups were composed of otters related at all levels of kinship, and otters that were more social did not interact with more highly related individuals.
5. There was no difference in direct or indirect reproductive success between social and nonsocial otters. Neither was there evidence that larger males had more offspring, nor that larger males were more social. We conclude that sociality did not result in reduced reproductive success, and that larger size in male otters did not confer an advantage (i.e., greater reproductive success).
6. Neither kin selection nor sexual selection for morphological characteristics were major factors influencing formation of social groups among coastal river otters. Alternative factors (i.e., ecological benefits) that may influence social organisation in coastal river otters are discussed.

Key words: kin selection, *Lontra canadensis*, microsatellite DNA, reproductive success, sexual selection.

INTRODUCTION

Evolution of sociality among animals has been attributed to benefits gained relative to costs from group associations (Alcock 1993; Alexander 1974; Rubenstein 1978). Fitness

benefits have been hypothesised to occur directly, at the level of the individual, through maximised reproductive success (Williams 1966), or indirectly through reproductive success of related individuals (i.e., kin selection; Hamilton 1964). Reciprocity and mutualism (Connor 1995; Mesterton-Gibbons & Dugatkin 1992), and ecological benefits (e.g., reduced predation or increased access to resources; Alexander 1974) also may account for benefits of group living, and need not be mutually exclusive (Gompper & Wayne 1996; Hughes 1998). Costs associated with group living may include reproductive suppression (Armitage 1986), intraspecific competition for resources or reproductive opportunities, and increased potential for parasite and disease transmission (Alexander 1974; Wrangham & Rubenstein 1986).

Among mammals, sociality takes a number of forms. Both genders may be predominantly solitary or may occur in monogamous pairs (Eisenberg 1981). Females may be social and males solitary, or both genders may be social and occur in mixed or single-sex groups (Eisenberg 1981). Considerable variation in sociality occurs among carnivores (Gittleman 1989). Most small nocturnal carnivores are solitary and monogamous pair bonds are prevalent among canids (Gittleman 1989). Herpestidae live in mixed-sex groups (Creel 1996), and among Procyonidae, *Nasua narica* live in female-bonded groups, but males are solitary (Gompper 1996). Although most Felidae are solitary, *Panthera leo* are highly social (Gittleman 1989; Packer 1986), living in mixed-sex groups composed of related females and a male coalition (Packer *et al.* 1991).

Theory predicts that for kin selection to occur, individuals in social groups should be more related than if they were chosen at random from the population, and that

association with kin should yield some benefit. Kin selection has been invoked to explain sociality among female *P. leo* because larger groups have greater success in preventing the loss of a large carcass to conspecifics and related females raise their offspring communally to defend them against infanticidal males (Packer 1986). Competition occurs among coalitions of male lions to acquire a pride of females and larger coalitions are more successful at maintaining possession of a pride (Packer *et al.* 1991). As coalition size increases, variance in reproductive success occurs but nonreproducing males are generally related to those that sired offspring (Packer *et al.* 1991) thereby benefiting from group association via indirect fitness. Therefore, there is compelling evidence for kin selection and inclusive fitness (direct and indirect reproductive success) among *P. leo*.

Recently, we documented social organisation that is atypical for mammals in *Lontra canadensis* inhabiting marine environments of Prince William Sound, Alaska, USA (Blundell, Ben-David & Bowyer *in press a*, Rock *et al.* 1994, Testa *et al.* 1994). In our system, river otters exhibited high variability in sociality. Although some individuals remained solitary throughout the year, others occurred in large groups of up to 18 individuals (Blundell *et al.* 2000, *in press a*, Rock *et al.* 1994, Testa *et al.* 1994). We demonstrated that social groups were composed largely of males, whereas females were most often solitary (Blundell *et al. in press a*). Our data indicated that while some females briefly joined mixed-gender groups, males usually occurred in all-male groups for extended periods, although some males remained solitary (Blundell *et al. in press a*). This high sociality in males and solitary nature of females raised the question as to

whether association with kin might offer benefits to male otters similar to those experienced by male lions, and whether alliance with kin groups could explain differences in sociality among genders of coastal river otters.

To critically evaluate hypotheses of kin selection, reproductive success should be measured (Armitage 1986; Hamilton 1964). Nonetheless, few studies have evaluated some measure of direct or indirect reproductive success in concert with degree of relatedness within and among social groups, and only five studies reported evidence of kin selection. Amos *et al.* (1993) noted that pods of *Globicephala melas* were highly related, but related males did not mate within the pods; opportunities for males to mate likely occurred when pods temporarily met during fission-fusion events. At other times, males could assist in raising related individuals within the natal pod by assisting with predator defence and cooperative feeding strategies, thereby increasing their indirect fitness (Amos *et al.* 1993). *Helogale parvula* occurred in highly related packs (Keane *et al.* 1994). Although dominant individuals in those mongoose packs produced most of the offspring, subordinate individuals of both sexes also reproduced, thereby gaining both direct and indirect fitness as a result of pack associations. Pusenius *et al.* (1998) reported higher reproductive success for *Microtus agrestis* among females breeding in kin clusters or near related individuals. Girman *et al.* (1997) noted high relatedness among individuals in packs of *Lycaon pictus*, with the unrelated alpha pair producing most of the offspring within the pack. Parallel reproductive strategies were reported for *Canis lupus* (Gompper & Wayne 1996).

In this study, we used molecular and behavioural data to examine the role of kinship in defining sociality and spatial relationships amongst river otters inhabiting marine environments in Prince William Sound, Alaska, USA. We tested the hypothesis that if kin selection defined social or spatial organisation among coastal river otters, otters would be more likely to interact with related individuals, and, because ecological and reproductive constraints affect the sexes differently (Wrangham and Rubenstein, 1986), that such interactions would differ between genders. Furthermore, we asked the question: Does association with a group have a cost in terms of reproductive success? We predicted that if only a few individuals in a social group produced offspring (i.e., benefited via direct reproductive success), otters in social groups should be related such that nonreproducing members would benefit from group association through indirect reproductive success (i.e., kin selection). Accordingly, we assessed direct reproductive success by determining parentage for otters and compared reproductive success between social and nonsocial otters. Additionally, we evaluated an index of indirect reproductive success by assessing the proportion of otters in the population related by increasing degrees of kinship for social compared with nonsocial otters. We hypothesised that if sociality entailed a reproductive cost, social otters would have fewer offspring, and other relatives in the population should be more distantly related.

Alternatively, if hypotheses related to kin selection cannot explain social organisation in coastal river otters, we hypothesised that sexual selection might be operating to determine social organisation and reproductive success for male otters. Therefore, we predicted that if females selected larger males (Weatherhead & Boag 1995;

Cooper & Vitt 1993) or larger males gained access to more females (Lewis, Tirado & Sepulveda 2000; Haley, Deutsch & Le Boeuf 1994; Clutton-Brock, Albon, & Guinness 1988; Le Boeuf & Reiter 1988), larger males would have more offspring. Additionally, if sexual selection affected social organisation, and males became solitary only after having obtained sufficient size to gain access to more females, we predicted that solitary males would be larger than social males. Alternatively, if sociality conferred a size advantage, we predicted that social males would be larger and have more offspring.

METHODS

Study Area

Field research was conducted in Prince William Sound, Alaska, USA (Blundell *et al. in press a*) from 1996 through 1999. Otters were live-captured at seven sites in western Prince William Sound, spanning an area of approximately 4,800 km^2. Detailed descriptions of the study areas are provided in Ben-David *et al.* (1998) and Bowyer *et al.* (1995). Fieldwork was conducted in 1996 and 1997 in Jackpot, Ewan, and Paddy bays along Dangerous Passage (60° 20'N, 148° 10'W), and in Herring Bay and surrounding areas on northern Knight Island (60° 30'N, 147° 40'W). In 1998, otters were captured at Herring Bay, Eleanor Island (60° 32'N, 147° 37'W), Esther Passage (60° 53'N, 147° 55'W), Unakwik Inlet (60° 55'N, 147° 30'W), Wells Bay (60° 55'N, 147° 20'W), and Naked Island (60° 40'N, 147° 25'W).

Otter Capture and Processing

One-hundred and eleven individual river otters were captured from May through July in 1996 and 1997, and from mid-April through May in 1998, with No. 11 Sleepy Creek®

double-jaw leg-hold traps or with Hancock traps (Blundell *et al.* 1999). Otters were anaesthetised with Telazol® (9 mg/kg) administered by Telinject® darts with a blowgun, or by hand injection for otters captured in Hancock traps. The following morphological measures were obtained from each otter: body length, total length (nose to tip of tail), baculum length, and testicle width (mm), and body weight (kg). Age was estimated for each otter (juvenile, young adult, adult, and old adult) based on body mass and tooth wear and staining, and 7 mL of blood was drawn from the jugular vein for DNA analysis. All methods used in this research were approved by the Institutional Animal Care and Use Committee at University of Alaska Fairbanks and adhere to guidelines for animal care and use adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998). Further details on capture and handling are provided in Blundell *et al.* (1999) and Blundell *et al.* (2000).

Radiotelemetry and Sociality

Information on sociality and spatial relationships of river otters was obtained from radiotelemetry data, because behavioural observations of otters in our remote study areas were difficult to obtain (Blundell *et al. in press a*). Fifty-five otters were surgically implanted with hermetically sealed radiotransmitters (Blundell *et al.*, 2000). Otters receiving transmitters were captured in Dangerous Passage (Jackpot Bay and vicinity) in 1996 and 1997, on northern Knight Island (Herring Bay and vicinity) in 1997 and 1998, and at Eleanor Island in 1998. Otters were radiotracked for the duration of transmitter battery life; from 1996 through 1999 in Dangerous Passage, from 1997 through 1999 in Herring Bay, and from 1998 to 1999 at Eleanor Island (n = 2,230 total locations).

Otters were radiotracked mostly from a fixed-wing aircraft. Tracking occurred year-round, but locations were obtained with greater intensity in spring, during mating season, and summer when weather was more conducive to regular flights. Universal Transverse Mercator (UTM) coordinates of otter locations were recorded along with information on visual sightings. Composition of social groups was determined from telemetry locations. If two or more telemetered otters were detected at the same location, the pilot took extra care to determine whether they were together, or merely in the general vicinity of one another. Additional details on radiotelemetry procedures and determination of sociality are provided in Blundell *et al.* (*in press a*).

Sampling Density

An estimate of the proportion of animals captured (i.e., sampling density) and the proportion radiotagged, in the three study areas with radiotagged otters, was calculated based upon density estimates for river otters in Prince William Sound, Alaska, provided in Testa *et al.* (1994). The upper and lower confidence intervals (CI; Table 2.1) for estimated mean density of river otters per 100 km of shoreline, obtained in June 1990 were used (Testa *et al.* 1994). June estimates were used because our sampling occurred mostly in that month and seasonal fluctuations in density estimates were reported by Testa *et al.* (1994). Calculations of shoreline length were obtained for each of our study areas with ARCINFO (ESRI, Redlands, California, USA). Number of otters per kilometre shoreline was expressed as CI multiplied by shoreline length/100 (upper and lower CI = 28 and 60 otters/100 km, respectively). Proportion of otters captured and proportion radiotagged in each area was then estimated by dividing the number of

animals captured (or radiotagged) in each study area by the minimum and maximum estimates, multiplied by 100.

DNA Laboratory Procedures

DNA Extraction

DNA was extracted from frozen blood samples from 110 individual otters with a modification of a protocol described by Groves & Shields (1997). Samples were incubated overnight at 37°C in a standard lysis buffer and Proteinase K. Residual proteins were precipitated with a high-salt solution and chloroform. DNA subsequently was precipitated with isopropanol and washed with ethanol. After drying, DNA was resuspended in 10 mM Tris and stored at –40°C.

Microsatellite Markers

Nine microsatellite loci were screened for this study. These included seven tetranucleotide markers (701, 715, 733, 782, 801, 818 and 829) developed for *Lutra lutra* (Dallas and Piertney 1998; and J. Dallas *pers. comm.*) and two dinucleotide markers (Mvis075 and Mer022) developed for *Mustela vison* and *M. erminea* (Fleming, Ostrander & Cook 1999). All markers were polymorphic, resulting in individual microsatellite fingerprints for each of the river otters studied.

PCR

Amplifications of microsatellites were done in a GeneAmp PCR System 9600 (Perkin-Elmer) thermocycler. The 10 µL total reaction volumes contained 1 µL 10x reaction buffer (Perkin-Elmer), 1 µL 2mM dNTP's, 1.5 to 2.0 µl 25mM $MgCl_2$, 0.4 µl 10 mg/mL BSA, 0.4 µL of each 10 µM primer and 0.05 µL AmpliTaq (Perkin-Elmer). Some

reactions included a fluorescently labeled primer (FAM, TET, or HEX), whereas others used 0.03 μL fluorescently labeled dNTP's (R6G and R110, Perkin-Elmer). A touchdown PCR profile was used with annealing temperatures ranging from 63°C to 48°C and a total of 42 cycles. A final extension step of 72°C for 30 min was used for all reactions. All PCR products were visualised with UV light in 1.5% agarose gels stained with ethidium bromide.

Sizing of Alleles

Successful PCR reactions were resolved on an ABI 373S Automated Sequencer with GS350 TAMRA used as an internal size standard in each lane. Markers were co-loaded with up to six markers per lane, selected so that sizes and dye colours did not overlap. Data were sized in base pairs and analysed with ABI GeneScan 3.1 and Genotyper 2.1 software.

Data Analysis

Genetic Relatedness

The coefficient of relatedness (*R*) between dyads was calculated with program Kinship (Version 1.2 Goodnight, Queller & Poznansky 1994, Queller & Goodnight 1989, Queller, Strassmann & Hughes 1993). Similar analyses also were performed substituting log-likelihood values for coefficient of relatedness to determine whether results differed between those two measures. The trends obtained by using *R* or log-likelihood did not differ, thus only *R* values are reported.

To ascertain that sufficient loci were used to effectively assess relatedness, degree of resolution in *R* obtained with each additional locus was determined (Girman *et al.*

1997). Little change occurred in the Queller & Goodnight relatedness index (R) after eight loci (Fig. 2.1). Therefore, inclusion of additional loci beyond the nine that were used would not improve estimates of relatedness.

The distribution of R values among all otters for which we had genetic data (n = 110) was evaluated, without respect to sociality, to determine the overall degree of relatedness of river otters among and within populations. Additionally, average relatedness was determined, independently, for otters residing in each area that had radiotagged individuals (Herring and Jackpot bays, and Eleanor Island) and relatedness was compared among telemetered populations with a one-way analysis of variance (ANOVA). Because that analysis included numerous comparisons of R values between pairs of otters, resulting in data that were not independent, randomisations were conducted to minimise that bias. After the initial ANOVA, R values were randomly sorted 1,000 times and F statistics were calculated on each randomised data set. The values of randomisations were then compared with the original ANOVA results and the proportion of statistics from the randomised data that gave a value as large or larger than the observed value provided an unbiased estimate of the probability that the null hypothesis was true (Manly 1991). Code for ANOVA by randomisation was written in S-Plus for Windows (V. 4.5).

Because sociality only could be assessed for those otters that were equipped with radiotransmitters, the mean relatedness of each telemetered otter to all other individuals captured in the population in which that otter resided was assessed. Calculations were conducted to determine average relatedness of animals with which an otter associated

(i.e., associates), and average relatedness of otters with which a telemetered individual did not associate (i.e., nonassociates). Sociality and telemetry data on river otters were analysed in yearly increments to include one reproductive cycle and seasonal fluctuations in availability of prey. Data were analysed in annual increments because degree of sociality may differ between years for individual otters as a result of varying ecological or reproductive conditions (Blundell *et al. in press a*). Accordingly, a three-way ANOVA by randomisation was conducted to compare average relatedness of associates between genders, and among years and areas; that analysis was repeated again to compare nonassociates. Because power to detect differences among areas and between genders was low, separate one-way ANOVAs by randomisation also were conducted for each gender to compare the average relatedness of associates and nonassociates among areas. Finally, a paired *t*-test by randomisation was conducted to assess whether the relatedness of otters with which an individual associated differed from the average relatedness of animals with which it did not associate. Appropriate power calculations were conducted for nonsignificant *P*-values for all statistical analyses (Zar 1994).

Indices of Association

Composition of social groups was dynamic (i.e., the same individuals did not always occur in the same groups); therefore, an assessment of frequency of association was not possible with respect to entire social groups. Accordingly, we assessed dyad interactions because that metric afforded a more detailed evaluation of whether the relatedness of a pair influenced their spatial or temporal associations through time. Three different indices of association between dyads were assessed because our ability to obtain

behavioural observations for otters was limited (Blundell *et al. in press a*). By evaluating several measures of association derived in different manners, potential for bias was reduced, thereby increasing confidence in our conclusions.

Relative frequency (*f*) of association was calculated between dyads by determining how many times individual *i* occurred in association with individual *j* divided by the total number of times individual *i* was located ($\sum f_{ij} / \sum f_i$). Matrices of relative frequencies of dyad associations were obtained for all telemetered individuals for each year in each area.

Dynamic interactions between individuals were evaluated with RANGES V software (Kenward & Hodder 1996) to obtain a "cohesion" index that assessed the tendency of two individuals to be close together at the same time. The procedure uses a randomisation approach, determining the location of one individual at a point in time with respect to the location of the other individual in the dyad at the same time, relative to all possible locations for the second individual (Kenward & Hodder 1996, Kenward, Marcström & Karlbom 1993). The observed and possible distances are compared, and a single index is obtained for each pair of animals. Matrices based on geometric mean distances between individuals were obtained for each year in each area. Association values ranged from –1 to +1, providing a continuum between avoidance (negative values) and attraction (positive values) of individuals in each dyad (Kenward & Hodder 1996, Kenward *et al.* 1993).

Spatial Relationships

Home ranges were estimated and percentage of home-range overlap between dyads was calculated for each study area in each year with RANGES V software (Kenward & Hodder, 1996). Amongst radiotagged individuals, there were no instances in which otters from one study area interacted with animals from another study area. Estimates of 95% home ranges were obtained with fixed kernel analyses and the reference smoothing parameter (Blundell, Maier & Debevec, 2001) and core (50%) home ranges were estimated with fixed kernel analyses and least squares cross validation (LSCV) smoothing (Blundell *et al.*, 2001). Because otters generally confine their movements to the shoreline, measurement of kilometres of shoreline within home-range contours is a more appropriate measure of home-range size (Blundell *et al.* 2001; Bowyer *et al.* 1995; Sauer, Ben-David & Bowyer 1999). Nonetheless, shoreline estimates were highly correlated with area estimates (r = 0.96, Pearson correlation; Blundell *et al.* 2001) and contours generally centred on shorelines (Blundell *et al.* 2001). Thus, calculating the percent overlap of home-range area among otters provided a reasonable index of overlap of actual areas used.

Mantel Matrices Comparisons

Mantel tests (Lugon-Moulin et al. 1999; Manly 1991; Smouse, Long & Sokal 1986) were used to compare matrices of association indices with degree of relatedness (R), with Multreg software (available from J. Goudet). Matrices of home-range overlap, dynamic interactions, and relative frequency of association between dyads were individually

correlated with a matrix of the coefficient of relatedness between dyads. A total of 10,000 randomisations were conducted at each comparison.

Sociality and Relatedness

In the event that otters that spent more time in social groups were more likely to associate with related individuals, analyses were performed assessing average relatedness by degrees of sociality. In an earlier study, Blundell *et al.* (*in press a*) evaluated degrees of sociality by assessing the proportion of locations within a year in which an otter was located with other otters. Data were categorised by otters that were not known to be social, otters that showed low sociality (≤10% social locations), moderate sociality (11–50%), and otters that were highly social (>50%). In this study, relatedness of each social otter to all telemetered otters in their respective population was assessed with a one-way ANOVA by randomisation, comparing mean relatedness for otters in each category of sociality. That analysis allowed for an evaluation of the mean relatedness among all telemetered otters with which a telemetered animal had the possibility of associating, to assess whether otters that were not social were solitary because they had no relatives in the population with which to socialise. That analysis, however, did not indicate the degree of sociality and relatedness among individuals with which an otter interacted. Accordingly, relatedness of associates also was assessed with a one-way ANOVA by randomisation, comparing average relatedness of associates in the low, medium, and high categories of sociality (Blundell *et al. in press a*).

Direct Reproductive Success

Parentage was assigned with CERVUS software (Marshall *et al.* 1998; Slate, Marshall & Pemberton 2000), which uses a likelihood model and Monte-Carlo simulations to assess multiple candidate parents. In our study, there were no known parent-offspring relationships; consequently, parentage was determined based upon the most likely assignment of offspring to candidate parents. Because our samples were heavily male biased (n = 75 male otters, n = 35 females), candidate fathers were assessed prior to evaluating candidate mothers. Only those otters that were obviously young (juvenile) were considered as potential offspring. River otters are relatively long-lived (≤13 years in the wild; Docktor, Bowyer & Clark 1987) and most reproduce as 2-year olds (Docktor *et al.* 1987; Hamilton & Eadie 1964); thus, our approach likely excluded some adults from the analysis that may be offspring of other resident adults. Because we had only crude estimates of age for most otters we captured, we could not reliably distinguish between age of adults with sufficient accuracy to determine that potential parents were at least 2-3 years older than potential offspring. Therefore, we chose a conservative route, assigning parentage only for those otters that were too young to be parents and considering all other otters as potential parents.

To determine whether association with a group had a reproductive cost, the average percentage of locations that were social for each otter was compared with the number of putative offspring identified for each individual, evaluating each gender separately. Because there were several years of telemetry data for some individuals, and the extent of sociality varied among years, the average sociality among years was

calculated for each otter. The correlation (Spearman's rho) between average sociality and number of offspring was assessed because identifying which year of social data might pertain to the putative offspring identified is not possible. Additionally, to assess whether group size influenced reproductive success for males, the correlation of number of offspring and average group size for each social otter was determined with SPSS for Windows (V. 7.0).

Indirect Reproductive Success

The mean proportion of individuals related to each otter at increasing levels of relatedness (R) was used as a measure of indirect reproductive success to determine whether number of relatives in the population differed between social and asocial otters. We used standard subdivisions of R values (Hartl & Clark 1997; Avise 1994) to divide our relatedness index into six discrete categories (R <0.009, 0.01- 0.124, 0.125 – 0.24, 0.25 – 0.49, 0.5 – 0.69, >0.7) in a manner similar to Kapsalis & Berman (1996). We did not have genetic samples from a reference group of otters of known relationships with which to calibrate the relatedness coefficient (de Ruiter & Geffen 1998, Girman et al. 1997). Therefore, we do not suggest that an R-value of 0.5 necessarily implies a full sibling or parent-offspring relationship (Hartl & Clark 1997; Avise 1994), only that increasing R values indicate increasing degrees of relatedness (i.e., constitute a relatedness index). The proportion of individuals (i.e., number of individuals per relatedness category/total number of individuals sampled in the population) was calculated to adjust for differences in sampling density for each area.

If association with kin was a factor in group formation, and social otters accrued more benefits through indirect reproductive success by group association, social otters would have a higher proportion of related individuals in the population. More distantly related otters (i.e., lower *R* values) would likely be more indicative of indirect, rather than direct reproductive success. A two-way ANOVA by randomisation was conducted to compare social and asocial otters with respect to the proportion of related individuals occurring in each category of relatedness. That analysis was conducted twice: to assess the number of relatives for each otter among otters in the population in which the telemetered individual resided; and among all otters for which we had genetic data, to allow for dispersal of related individuals. Those analyses were conducted by entering social or nonsocial, and relatedness category as the independent variables, and mean proportion of related individuals occurring in each relatedness category as the dependent variable.

Sexual Selection

To determine whether social organisation in male otters was associated with sexual selection for larger males, multivariate analysis of variance (MANOVA; SPSS 7.0) was conducted to evaluate differences between social and nonsocial otters, entering six morphological characteristics (weight, body length, weight to total length ratio, baculum length, and testicle width) as dependent variables for male otters considered as candidate parents. To determine whether larger males had higher reproductive success, a linear-regression analysis was conducted evaluating data for those males identified as candidate parents. Number of offspring per individual (square-root transformed) was entered as the

dependent variable, and size parameters were entered as independent variables in a multiple regression with all variables entered simultaneously.

RESULTS

Sampling Density

A greater proportion (≥47%) of otters estimated to reside in each study area was captured in Herring Bay compared with Jackpot Bay and Eleanor Island (≥30 and 17 %, respectively; Table 2.1). Similarly, the proportion of the estimated density of otters that were radiotagged in Herring Bay also was greater (≥25%) compared with Jackpot Bay and Eleanor Island (≥24 and 17 %, respectively; Table 2.1).

Genetic Relatedness

Relatedness among river otters was generally low and the average *R* value was higher within telemetered populations than among all otters for which genetic data were available (Fig. 2.2). Average relatedness differed among telemetered populations; otters residing in the Jackpot Bay area were more highly related than otters in Herring Bay or Eleanor Island, which did not differ (Fig. 2.2)

A three-way ANOVA by randomisation detected no difference among areas ($F_{2,64} = 0.10$, $P = 0.91$), years ($F_{3,64} = 0.35$, $P = 0.79$), or between genders ($F_{1,64} = 1.9$, $P = 0.18$) in the average relatedness of associates (Fig. 2.3). There was a significant difference (Fig. 2.3) in mean relatedness of nonassociates among areas ($F_{2,64} = 3.3$, $P = 0.04$), but not among years ($F_{3,64} = 0.39$, $P = 0.75$), or between genders ($F_{1,64} = 0.02$, $P = 0.9$). In separate analyses by gender, no difference among areas occurred in average relatedness of associates ($F_{2,56} = 0.64$, $P = 0.52$ ANOVA by randomisation) or

nonassociates ($F_{2,56}$ = 1.39, P = 0.26 ANOVA by randomisation) for male river otters (Fig. 2.3). Similarly, there was no difference among areas in mean relatedness of otters that females associated with ($F_{2,9}$ = 0.96, P = 0.46 ANOVA by randomisation), but a difference was detected among areas in average relatedness of nonassociates (Fig. 2.3; $F_{2,9}$ = 7.2, P = 0.02 ANOVA by randomisation). Mean relatedness of nonassociates for females was similar between Eleanor Island and Herring Bay (P = 0.7, post-hoc Scheffe), and between Herring and Jackpot bays (P = 0.07, post-hoc Scheffe), but Jackpot Bay and Eleanor Island differed (Fig. 2.3; P = 0.01, post-hoc Scheffe). A paired comparison, by individual, of mean relatedness of associates compared with nonassociates noted no difference for male otters (t_{32} = 1.8, P = 0.08); power to detect a difference was high (power = 0.91). Mean relatedness of associates differed from that of nonassociates for female otters (t_9 = 2.6, P = 0.03); nonassociates were less related than associates at Eleanor Island (Fig. 2.3).

Relatedness and Indices of Dyad Associations

Degree of relatedness within pairs of individuals did not affect spatial or temporal interactions. There was no correlation between any of the association indices and genetic relatedness (Fig. 2.4). There was variation among study areas and years but randomisation probabilities for all indices ranged from 0.15 to 1.0 and the highest r^2 equalled 0.08.

Relatedness by Sociality Category

Degree of sociality (i.e., the proportion of locations in a year in which an otter occurred with other otters; Blundell *et al. in press a*) did not have an effect on whether an otter was

more likely to socialise with relatives (Fig. 2.5). When mean coefficient of relatedness of otters in each category of sociality (none, low, moderate and high) was compared among all telemetered otters in the resident population, there was no difference in the mean relatedness among otters with which an individual had the potential of associating (Fig. 2.5a). Similarly, when mean relatedness of only those individuals with which otters actually associated was evaluated, there also was no difference in level of relatedness amongst categories of sociality (Fig. 2.5b).

Direct Reproductive Success

Parentage was assigned for 53 young otters. LOD scores (logarithm of the likelihood ratio) ranged from 0.79 to 8.03 ($\bar{x}$ = 3.2, SD = 1.5). Delta values (difference in LOD scores between most likely and second most likely parent) ranged from 0.34 to 5.35 ($\bar{x}$ = 1.75, SD = 1.34). A total of 67.3% of parent-offspring trios were assigned at the 95% confidence level and 32.7% were assigned with 80% confidence. Offspring were identified for 87.5% of 21 male otters and 91.5% of 12 females that were radiotagged and considered as candidate parents. There was no correlation between number of putative offspring and proportion of locations spent social for either gender (Fig. 2.6). Similarly, there was no correlation (r = 0.31, P = 0.17, Spearman's rho) between number of offspring and average group size among telemetered male otters considered as candidate parents (overall mean group size = 2.9, SD = 1.1).

Indirect Reproductive Success

The mean proportion of relatives occurring in each relatedness category did not differ among resident populations between social and asocial otters (Fig. 2.7a). Similarly, there

was no difference between social and nonsocial otters in mean proportion of relatives in each relatedness category among all otters for which we had genetic data (Fig. 2.7b), indicating that association with a group conferred no advantage with respect to indirect reproductive success. Independent of sociality, the proportion of relatives occurring in each category of relatedness was significantly different for both analyses (Fig. 2.7).

Sexual Selection

Among male otters considered as candidate parents, social otters were neither larger, nor smaller than nonsocial otters (Table 2.2). Similarly, the regression of square-root transformed number of offspring against morphological features for male otters was not significant ($F_{5,20} = 2.1$, $P = 0.13$, adjusted $R^2 = 0.2$), indicating that larger otters did not have more offspring.

DISCUSSION

Kinship does not appear to influence social organisation and spatial relationships in *L. canadensis* in Prince William Sound. Indeed, the average coefficient of relatedness among members of otter social groups (Fig. 2.3) was low compared with mean relatedness of social groups for other carnivores: *Helogale parvula* $R = 0.33$ (Creel & Waser 1994); *Crocuta crocuta* $R = 0.31$ (Mills 1985); *Hyaeana brunnea* $R = 0.26$ (Mills 1990); *Vulpes vulpes* $R = 0.38$ (Macdonald 1979) and *P. leo* (lionesses) $R = 0.25 - 0.50$ (Packer *et al.* 1991).

In some carnivores, group associations or interactions between individuals were kin-based (Gompper *et al.* 1997; Girman *et al.* 1997; Keane *et al.* 1994; Packer *et al.* 1991), affording the potential for cooperative behaviour and enhancement of fitness of

related individuals. In contrast, regardless of whether we assessed the structure of groups of social otters (Figs. 2.3 and 2.5), or the interactions among dyads (Fig. 2.4), degree of relatedness did not influence the extent of sociality or spatial proximity.

Among social animals, variance in mean relatedness (R values) of individuals with which a river otter socialised was high (Fig. 2.3); social groups were composed of individuals that were not related as well as otters that were highly related ($R \leq 0.7$). Moreover, there was no indication that otters selected highly related individuals with which to socialise, as evidenced by the similarity in mean relatedness of associates and nonassociates (Fig. 2.3). That female otters at Eleanor Island associated with more highly related individuals compared with other areas, and in contrast to males, is likely a function of sampling density in that area. We captured and radiotagged only two females at Eleanor Island (Table 2.1) and likely do not have a representative sample for that gender in that area.

Furthermore, individuals that spent more time in social groups did not associate with more highly related individuals (Fig. 2.6), again indicating no preference for association with individuals with higher degrees of kinship. Our estimates of sociality, based upon telemetry data, may represent underestimates because only one-quarter to one-half of the estimated density of otters in Jackpot and Herring bays was radiotagged, and approximately one-third of the estimated density at Eleanor Island (Table 2.1). Although visual observations were infrequent and telemetered otters may have been travelling with unmarked animals, most observations confirmed that radiotagged otters were not travelling with unmarked individuals, and established the incidence of solitary

individuals (Blundell *et al. in press a*). Therefore, telemetry observations likely represent a reasonable estimate of sociality (minimum group size) in coastal river otters.

In contrast to other studies in which, as a result of gender-biased dispersal, related individuals (predominantly females) had a tendency to occupy nearby or overlapping home ranges (Albon *et al.* 1992; King 1989; Pusenius *et al.* 1998; Sera & Gaines 1994), we observed no such relation. Overlap of 95% home ranges might occur between unrelated individuals without the need for direct interactions, but intensive core areas of use (i.e., 50% home ranges) may have a higher probability of being maintained as exclusive (Kruuk & Moorehouse 1991), or perhaps shared among relatives. We noted no association, however, between relatedness and overlap of either 95% (Fig. 2.4c) or 50% home ranges (Fig. 2.4d). Therefore, our conclusions are the same whether we evaluated the structure of social groups or interactions among dyads – sociality and spatial relationships in coastal river otters in Prince William Sound were not kin-based.

There also was no obvious cost to sociality in terms of reproductive success. Group size was unrelated to reproductive success, and we detected no differences in our measures of direct (Fig. 2.6) or indirect reproductive success (Fig. 2.7) between social and nonsocial animals. Despite some variation between areas, our overall results indicated that sociality did not incur a reproductive cost for coastal river otters. Likewise, sociality did not confer a benefit in terms of indirect reproductive success (Hamilton 1964). Therefore, we reject kin selection as the basis for formation of social groups among coastal river otters. Similarly, we observed no evidence that sexual selection, with respect to phenotypic characteristics of males, influenced social organisation for

coastal river otters. Male otters that were social were neither larger nor smaller than nonsocial males (Table 2.2).

In contrast to many studies in which larger males had greater reproductive success (Lewis *et al.* 2000; Weatherhead & Boag 1995; Haley *et al.* 1994; Cooper & Vitt 1993), in our system, size had no apparent bearing on reproductive success or sociality in coastal river otters. Larger males did not have greater reproductive success, irrespective of sociality, suggesting that selection by females for larger males may not occur. Data reviewed in Clutton-Brock (1988) indicated that phenotypic characteristics are unlikely to be the only reason for variance in mating success. There also was no indication amongst studies reviewed (Clutton-Brock 1988) that direct competition between males would be intense or that evolution of secondary sexual characteristics would necessarily be favoured by selection. Other factors, as yet unidentified, likely influence reproductive success among coastal river otters

In other studies, alternative explanations for spatial or social associations were offered. Surridge, Bell & Hewitt (1999) reported that related individuals did not necessarily form kin groups in *Oryctolagus cuniculus*; behavioural data were more suggestive of optimal group size as the factor influencing social organisation. Ecological influences such as distribution and abundance of critical resources, intensity of predation, and inter- and intra-specific competition directly affect social organisation (Alexander 1974; Wrangham & Rubenstein 1986), often resulting in a trade-off between costs and benefits of sociality (Alcock 1993; Mangel 1990).

In an earlier study (Blundell *et al. in press a*), we reported that otters in social groups had better-quality diets that were higher in pelagic fishes, compared with otters that showed little or no sociality. Benefits of group association for otters in Prince William Sound likely included cooperative foraging to increase individual capture success when preying upon schooling pelagic fishes. Otters that were more social also had smaller home ranges, suggesting greater efficiency in foraging; further evidence that the benefits of social behaviour for river otters may have been cooperative foraging (Blundell *et al. in press a*). Although we could not critically evaluate predation pressure, that more social otters specialised in better-quality prey was indicative of a benefit of sociality, whereas simple avoidance of predation would not have resulted in differential diets between otters with varying degrees of sociality (Blundell *et al. in press a*).

Cooperation with kin would not be essential for a river otter to increase its access to higher–quality prey. Large schools of pelagic fishes enter the nearshore system where otters forage (Ben-David *et al.* 1996; Bowyer *et al.* 1994) after the cessation of the mating season (Blundell *et al. in press a*). When available in the nearshore environment, pelagic fishes aggregate in such abundance (Brown, Wang, & Vaughan 1999; Groot & Margolis 1991; Maniscalco, Ostrand & Coyle 1998) that intra-specific competition is nil because rich patches of prey cannot be exploited in a single feeding (Blundell *et al. in press a*). Although a group of predators may work together to contain a school of fishes (Norris & Schilt 1988), each group member forages as an individual, capturing its own prey (Packer 1988). Thus, individual selection (i.e., increased access to better-quality diet, which may translate to higher nutritional reserves necessary for successful

reproduction; Robbins 1983; Bronson 1989) may operate within a social group, independent of any relationship among group members. That we detected no difference in the more dynamic morphological parameters (e.g., body weight) when comparing social and nonsocial otters is not surprising given that otters were captured prior to the arrival of pelagic fishes in the nearshore environment. Male otters that were social and obtained better-quality diets the previous summer may overwinter in better condition than solitary otters and may thus have more energy reserves during mating season (Bronson 1989). Such reserves may not be evident in the morphological features we measured, because none evaluated body condition. Therefore, sociality may confer a benefit in terms of increased body condition through better quality diets (Blundell *et al. in press a*), and data currently available for coastal river otters indicate that sociality does not incur a cost in terms of reduced reproductive success. Kin selection among social groups, therefore, is not essential to compensate for a reduction in reproductive success or to increase individual fitness.

Moreover, timing of prey availability further eliminates the need for kin-based social groups among male otters. Male mating coalitions do not occur among coastal river otters (Blundell *et al. in press a*) and some males leave social groups for the duration of mating season (Blundell *et al. in review*), rejoining the group prior to the arrival of pelagic fishes (Blundell *et al. in press a*). Female river otters likely have fewer opportunities to take advantage of cooperative foraging because reproductive adults are attending to altricial offspring during seasonal availability of schooling fishes in the environment (Blundell *et al. in press a*). Thus, females tend toward solitary behaviour

although the occurrence of helping behaviour from another female has been observed (Rock *et al.* 1994).

The occurrence of solitary males among coastal river otters, however, remains a mystery (Blundell *et al. in press a*). If sociality results in a better-quality diet and does not have a cost in terms of reproductive success, all males should be social. Competition for elusive reproductive females, which undergo synchronous oestrus and do not aggregate, may be intense among males, leading to an avoidance of other males during mating season (Wrangham & Rubenstein 1986). Timing of prey availability in this system naturally accommodates a seasonal change in social structure (Blundell *et al. in press a*), thereby permitting males to gain the benefits of sociality (cooperative foraging) without incurring a cost in terms of reproductive success. Ultimately, female distribution defines that of males and strategies of males may be altered as a trade-off between reproductive success and ecological benefits (Wrangham & Rubenstien 1986), or more than one mating strategy may be successful (Andersson 1994).

Mating scars are prevalent among female otters during oestrus (Blundell pers. obs.; Toweill & Tabor 1982); thus, risk of injury to oestrous females may be high and a female may be reticent to accept the attentions of a male with which she is unfamiliar. We hypothesise that frequent encounters with solitary males outside of mating season may increase the likelihood of a male being accepted by a female when she is in oestrus. Therefore, males may forego opportunities for cooperative foraging in favour of increased opportunities for contact with females outside of mating season, which may result in increased reproductive opportunities.

Perhaps among coastal river otters, solitary males obtain more mating opportunities, but our data may have been insufficient to elucidate that effect. River otters have delayed implantation (Hamilton & Eadie 1964), giving birth almost 1 year after mating occurred (Blundell *et al. in press a*; Noll 1988,). Our fieldwork was conducted during mating season when coastal river otters were most easily captured at latrine sites (Blundell *et al.* 1999), but when young of the year remained sequestered in natal dens. Thus, there is a 2-year delay between a mating event and our ability to capture the resultant offspring. Offspring of previous years may have dispersed into areas for which we had no genetic data. Therefore, our study provides preliminary insights into the mating system of coastal river otters, but our ability to completely assess reproductive success of solitary versus social males during a 3-year study is limited. To fully understand social organisation or mating systems requires long-term studies such as those conducted on mongooses (Creel 1996; Creel & Waser 1994; Rood 1978, 1990), hyenas (Kruuk 1972, Frank 1996 & Mills 1996), and lions (Packer & Pusey 1982; Packer *et al.* 1991). Unquestionably, there are factors that define social organisation and reproductive opportunities among coastal river otters that have not been identified, in particular the phenomenon of solitary males, and further investigations are needed.

In conclusion, our data permit an unqualified rejection of kinship as a factor in determining sociality or spatial relationships in *L. canadensis* inhabiting marine environments. Additionally, we did not find evidence that larger males had more offspring, indicating sexual selection with respect to phenotypic characteristics also may not influence social organisation of river otters. Our study provided further evidence that

an increase in individual fitness is likely obtained via ecological benefits (i.e., cooperative foraging), thereby potentially explaining the function of sociality among coastal river otters (Blundell *et al. in press a*).

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Table 2.1. Estimates of density and total proportion (in parentheses) of river otters captured and radiotagged in each study area in Prince William Sound, Alaska, USA, from 1996 to 1998. Estimates are based upon upper and lower confidence intervals for estimates of mean density of river otters in Prince William Sound in June 1990 (Testa *et al.* 1994).

Variable	Jackpot Bay	Herring Bay	Eleanor Island
Size of area (km shoreline)	172.8	138.6	88. 0
Number of males captured	20	25	7
Number of males radiotagged	17	16	7
Number of females captured	11	14	2
Number of females radiotagged	8	5	2
Lower estimated density[A] captured	48 (64.1)	39 (100)	25 (36.5)
Proportion radiotagged	51.7	54.1	36.5
Upper estimated density[B] captured	104 (29.9)	83 (46.9)	53 (17.1)
Proportion radiotagged	24.1	25.3	17.1

[A] 28 otters/100 km

[B] 60 otters/100 km

Table 2.2. A comparison of morphological and reproductive features among male river otters in Prince William Sound, Alaska, USA, with respect to sociality. Overall model *P*-value for the MANOVA assessing sociality and morphological characteristics was not significant ($P = 0.35$). Otters included in this analysis were adult males considered as candidate parents.

	SOCIAL ($n = 14$)		NONSOCIAL ($n = 7$)	
Variables	$\bar{x}$	SD	$\bar{x}$	SD
Body Length (mm)	812.1	47.6	842.7	44.0
Weight (kg)	9.6	0.8	10.6	0.6
Weight-Length Ratio (weight /total length x 1000)	7.3	0.6	7.8	0.5
Testicle Width (mm)	53.8	6.3	53.0	5.4
Baculum (mm)	118.6	14.3	120.7	11.4
Number of Offspring	1.9	1.3	1.3	1.1

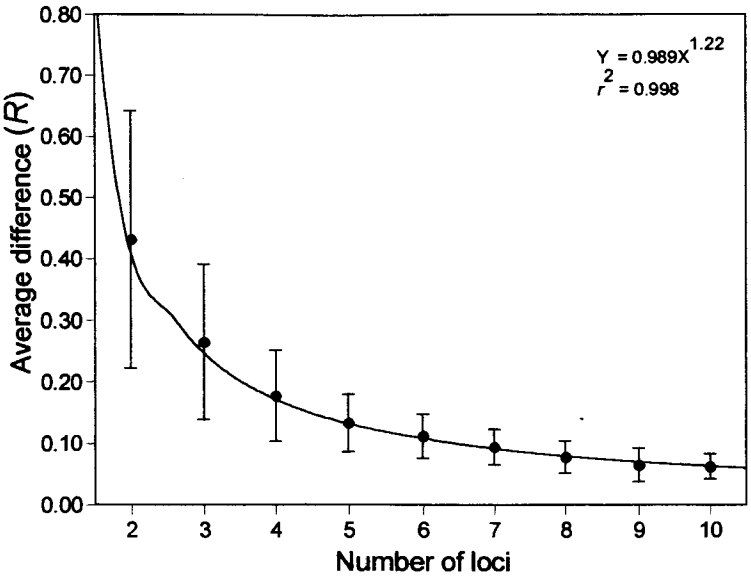

Figure 2.1 - An assessment of the degree of resolution obtained in the coefficient of relatedness (R) with the addition of each new locus into the analysis for river otters captured in Prince William Sound, Alaska, USA, from 1996 to 1998. Error bars are standard deviation.

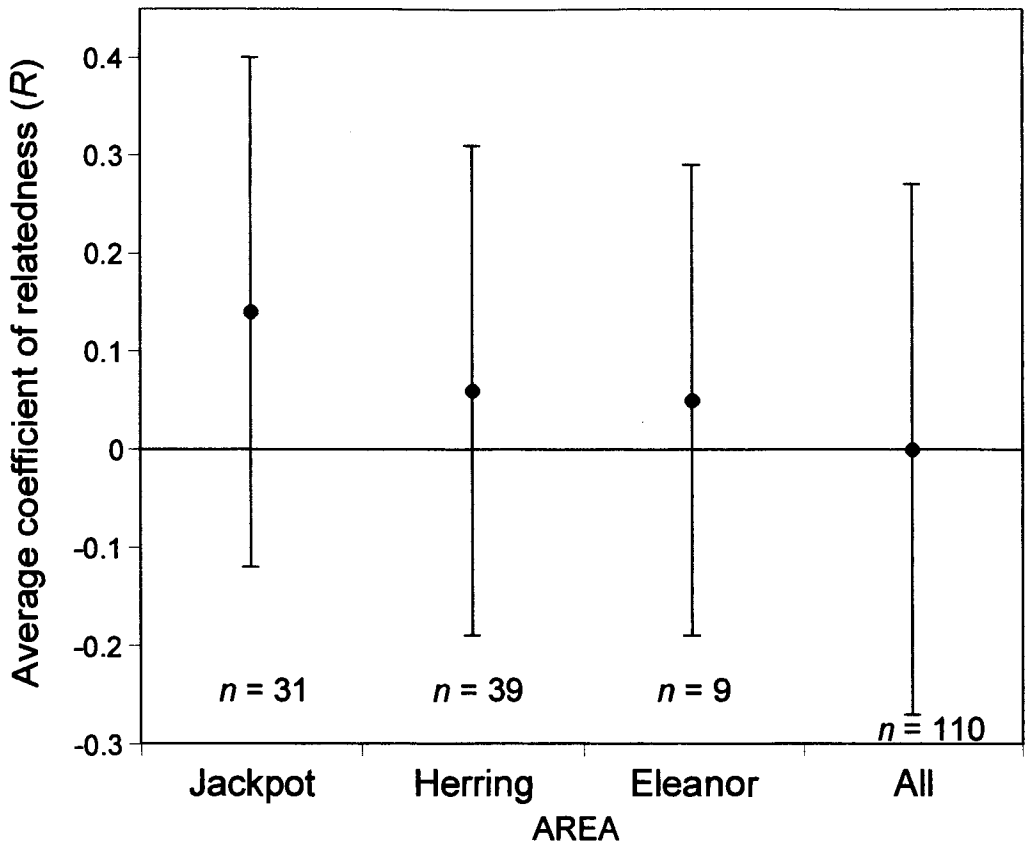

Figure 2.2 - A comparison of the coefficient of relatedness (R) for all river otters captured in the study areas in Prince William Sound, Alaska, for which we also had radiotelemetry data (Jackpot and Herring bays and Eleanor Island) and the R-value for all otters captured in this study (seven areas). Error bars are standard deviation. Average relatedness differed among telemetered populations ($F_{2,2473} = 32.3$, $P < 0.001$ ANOVA by randomisation); otters residing in the Jackpot Bay area were more highly related ($P \leq 0.02$ Scheffe post-hoc comparisons) than otters in Herring Bay or Eleanor Island, which did not differ in average relatedness (Fig. 2; $P = 0.9$ Scheffe)

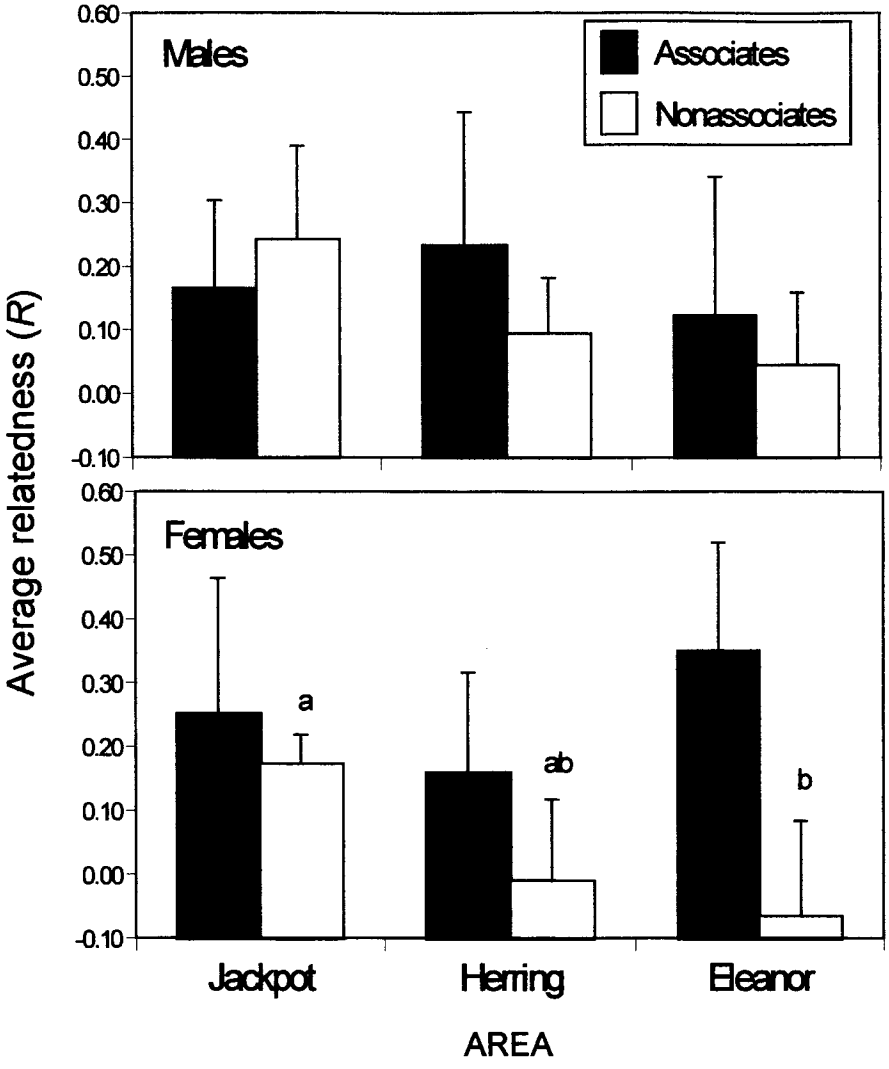

Figure 2.3 - An assessment, by gender, of the average relatedness ($R \pm$ SD) of radiotagged otters in Prince William Sound, Alaska (1996- 1999) to river otters with which they associated (i.e., associates), compared with relatedness of individuals with which they did not associate (i.e., nonassociates). There was no difference for any analysis of relatedness of associates or nonassociates for male otters (top) but the relatedness of female otters (bottom) differed by area for nonassociates. Different letters indicate significant differences between areas (i.e., Jackpot and Herring bays, and Herring Bay and Eleanor Island did not differ, but Jackpot Bay and Eleanor Island were significantly different).

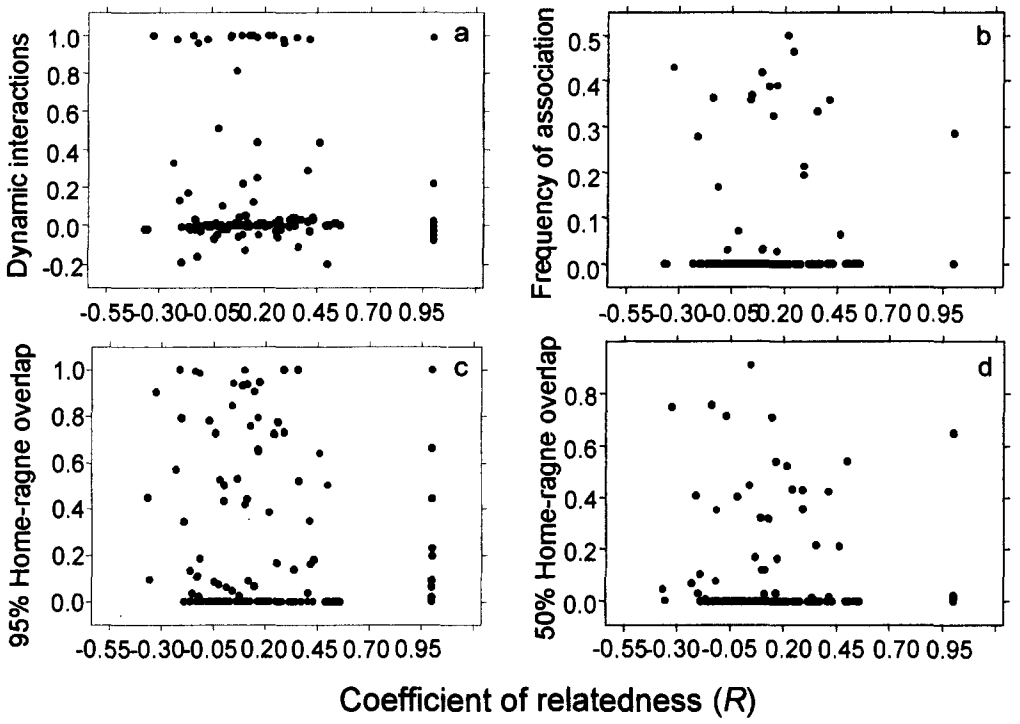

Figure 2.4 - A comparison of relatedness (R) with indices of association between dyads for Herring Bay (n = 17 otters), Prince William Sound, Alaska, in 1998. Dynamic interactions (**a**) indicate proximity of temporal-spatial locations; negative values indicate avoidance, zero indicates not different from random, and increasing positive values indicate more time spent in association (1 = always together). Frequency of association (**b**) is a relative measure of the number of times otter i was located with otter j divided by total number of locations for otter i ($\sum f_{ij}/\sum f_i$). The percent overlap of 95% (**c**) and 50% (**d**) home ranges indicate the spatial relationship of otters. There was no correlation between relatedness and any index of association in any year or study area. Data from Herring Bay, 1998, are shown here because a larger number of otters in that year offered greater potential of demonstrating any correlation between relatedness and indices of association.

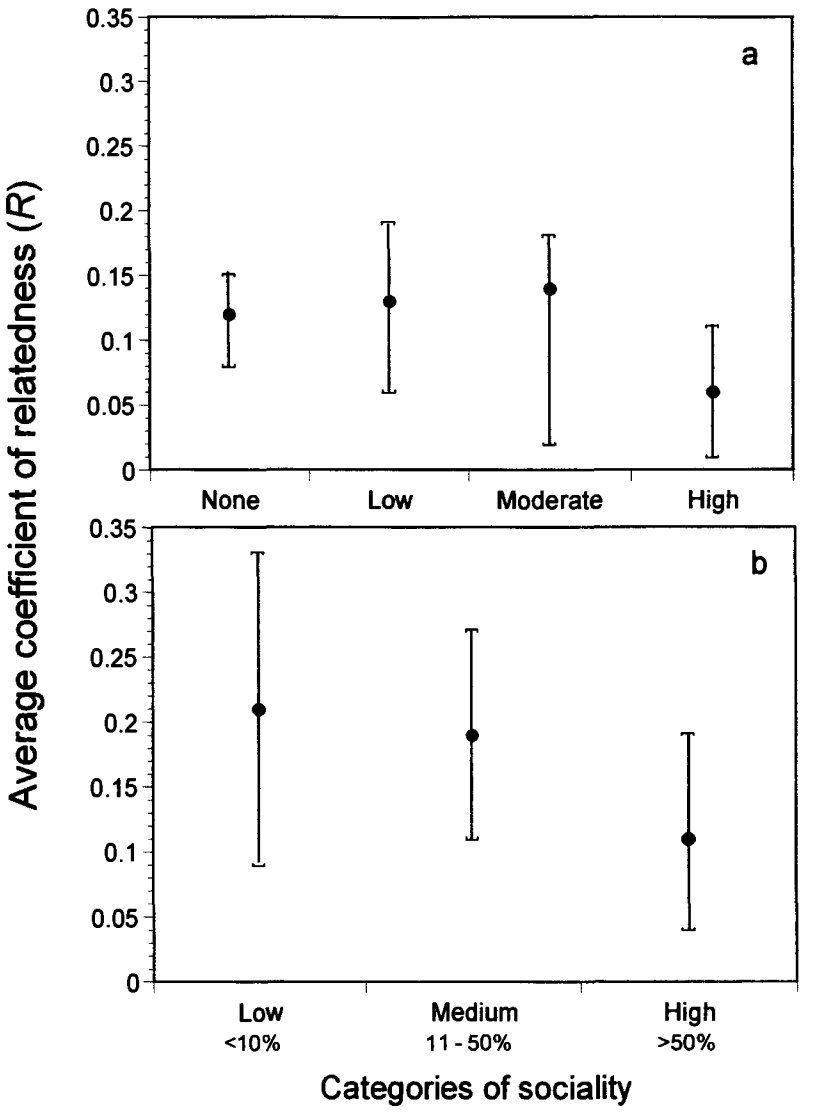

Figure2.5 - An assessment of the degree of sociality (i.e., the proportion of locations in a year in which an otter occurred with ≥ one other individual) and the mean relatedness ($R \pm$ SD) with all other telemetered individuals within the resident population (**a**) and the relatedness of individuals an otter actually associated with (**b**). There was no difference in relatedness of otters among categories of sociality for all telemetered otters ($F_{3,103} = 2.5$, $P = 0.07$ ANOVA by randomisation) or among sociality categories for otters associated with ($F_{2,67} = 1.7$, $P = 0.19$ ANOVA by randomisation).

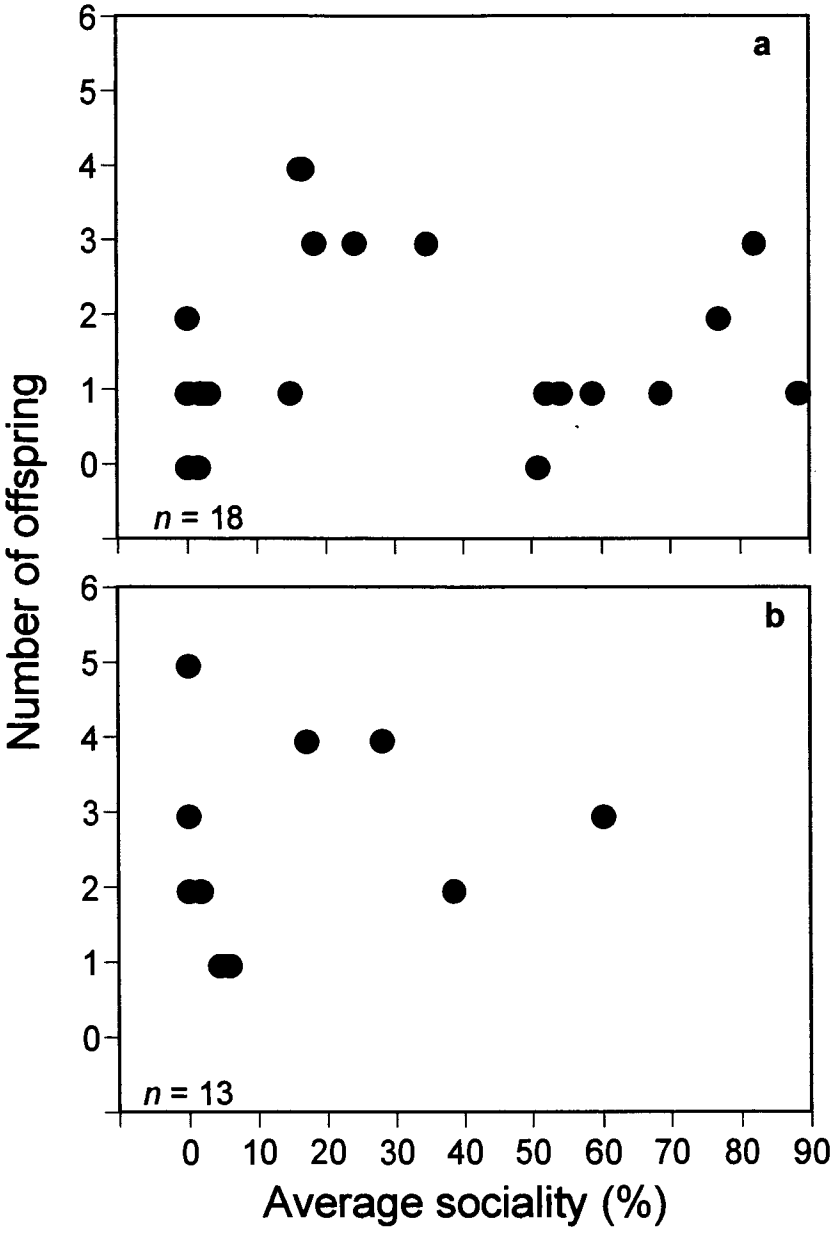

Figure 2.6 - An evaluation of direct fitness, comparing the degree of sociality (average percent of social locations among all years for each social otter) with the number of offspring for which the otter was identified as a parent. There was no correlation between sociality and number of offspring for male ($r = 0.31$, $P = 0.17$, Spearman's rho) or female otters ($r = -0.01$, $P = 0.99$, Spearman's rho).

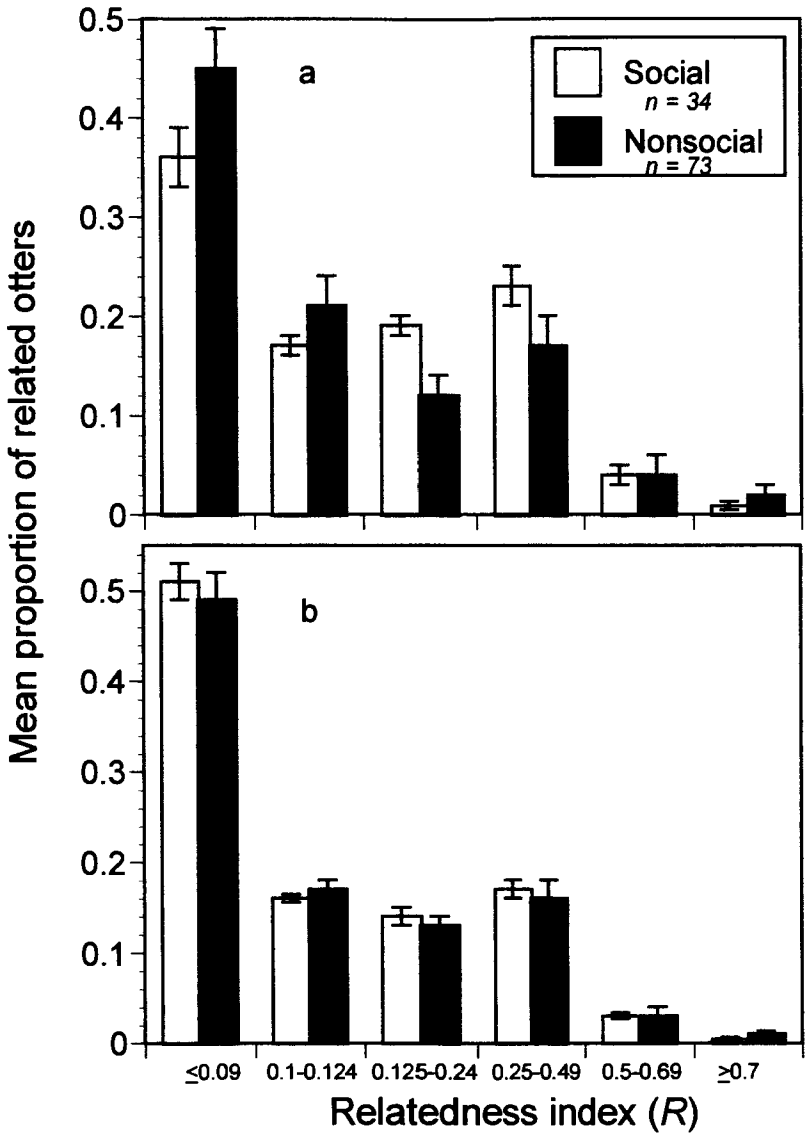

Figure 2.7 - An evaluation of indirect fitness, comparing the mean proportion (± SD) of relatives occurring in each relatedness category, between social and nonsocial otters, among resident populations (**a**), and that comparison among all populations (**b**). There was no difference in mean proportion of relatives per category between social and nonsocial otters in resident populations (**a**; $F_{1,635} = 0.0006$, $P = 0.99$, ANOVA by randomisation), or among all populations (**b**; $F_{1,641} = 0.0015$, $P = 0.97$, ANOVA by randomisation), but the proportion of relatives occurring in each category of relatedness was significantly different for both analyses (**a** and **b**; $F_{5,635} \geq 152.0$, $P < 0.001$).

CHAPTER 3

Sex-biased dispersal and gene flow in coastal river otters: implications for natural recolonization of extirpated populations[3]

ABSTRACT: River otters (*Lontra canadensis*) were extirpated from much of their historic distribution because of exposure to pollution and urbanization, resulting in expansive reintroduction programs that continue today for this and other species of otters worldwide. Bioaccumulation of toxins negatively affects fecundity among mustelids, but high vagility and different dispersal distances between genders may permit otter populations to recover from extirpation caused by localized environmental pollution. Without understanding the influence of factors such as social structure and sex-biased dispersal on genetic variation and gene flow among populations, effects of local extirpation and potential for natural recolonization (i.e., the need for translocations) cannot be assessed. We studied gene flow among seven study areas for river otters (n = 110 otters) inhabiting marine environments in Prince William Sound, Alaska, USA, and hypothesized that sociality would influence genetic structure of populations. With nine DNA microsatellite markers and assignment tests, we calculated immigration rates and dispersal distances, and tested for isolation by distance. We radiotracked 55 individuals in three areas to determine characteristics of dispersal. Gender differences in sociality and spatial relationships resulted in different dispersal distances. Male river otters had greater gene flow among close populations (within 16-30 km) via breeding and

[3] G. M. Blundell, M. Ben-David, P. Groves, R. T. Bowyer, and E. Geffen. In Review. Sex-biased dispersal and gene flow in coastal river otters: implications for natural recolonization of extirpated populations. Conservation Biology.

natal dispersal, but both genders exhibited an equal, low probability of natal dispersal; and some females dispersed 60-90 km. These data, obtained in a coastal environment without anthropogenic barriers to dispersal (e.g., habitat fragmentation or urbanization), may serve as baseline data for predicting dispersal under optimal conditions. Our data indicate that natural recolonization of coastal river otters following local extirpation would be a slow process because of low dispersal among females, and recolonization is unlikely unless viable populations occurred within 60 km. Because of significant isolation by distance for male otters and low gene flow for females, translocations should be undertaken with caution to help preserve genetic diversity in this species.

INTRODUCTION

River otters (*Lontra canadensis*) are piscivorous predators, which forage near the apex of the trophic pyramid and readily accumulate high levels of pollutants (Hill & Lovett 1975; Clark et al. 1981; Henney et al. 1981; O'Connor & Nielson 1981; Francis & Bennett 1994; Halbrook et al. 1994; Duffy et al. 1994, 1996, 1998; Taylor et al. 2000; Ben-David et al. in press *a*, *b*). Indeed, river otters in North America were reduced throughout much of their historic range in the eastern and midwestern United States by the early 1900s because of pollution, urbanization, and overharvest (Serfass et al. 1993; Larivière and Walton 1998). Consequently, numerous projects were initiated to reintroduce river otters to areas from which they were extirpated (Erickson and McCullough 1987; Polechla 1990; Ralls 1990; Serfass et al. 1993; Hartup et al. 1999). Translocation projects are currently underway in the United States, and other projects are being considered (T. L.

Serfass; North American Continental Representative for the IUCN Otter Specialist Group, personal communication).

Because of their susceptibility to pollution, this mustelid recently has been recognized as an indicator of environmental health in aquatic ecosystems (Melquist & Dronkert 1987; Duffy et al. 1996; Larivière & Walton 1998), but comparatively little is known about their ecology. Without a more complete understanding of population dynamics and how factors such as social structure, mating system, or sex-biased dispersal influence genetic variation and gene flow among populations (Shields 1987; Avise 1994; Storz 1999), effects of local extirpation and the potential for natural recolonization, indeed, the need for reintroduction projects cannot be assessed.

We studied genetic diversity and patterns of space use among populations of river otters inhabiting marine environments in wilderness areas of Prince William Sound, Alaska, USA, to determine characteristics of sex-biased dispersal and gene flow in an environment without anthropogenic (e.g., habitat fragmentation or urbanization) barriers to dispersal. Data from this study may serve as a baseline for predicting dispersal of otters under optimal conditions. Such data may be incorporated into models estimating the likelihood of natural recolonization from nearby populations, or may be useful for modeling population expansion for current otter reintroduction projects, and when future translocation of river otters is considered.

We hypothesized that coastal river otters occurred in genetically distinct populations and that genetic differentiation was mediated by sex-biased dispersal. Among most species of mammals, females show philopatry, whereas males are more

likely to disperse from their natal area (Greenwood 1980; Shields 1987). Accordingly, with microsatellite DNA, we tested the hypothesis that female otters within a population would be more related to each other than to males in that population. We also hypothesized that male otters within a population would be more related to other males (if sibling groups disperse together) than to females. For both genders, we hypothesized that relatedness of otters would be higher within than among populations.

Additionally, we tested the hypothesis of isolation by distance, predicting that genetic differentiation among populations would increase with increasing geographic distance and that the effect would be more pronounced for females, if dispersal was male-biased. Similarly, we used assignment tests (Cornuet et al. 1999) to estimate immigration rates and dispersal distances in conjunction with telemetry data. We also evaluated the effects of sociality on genetic structure within populations, hypothesizing that populations in which otters were more social also would be populations that potentially were more inbred.

METHODS

Study Areas

Study areas were located throughout western Prince William Sound, spanning an area of approximately 4,800 km^2 (Fig. 3.1). Fieldwork was conducted in 1996 and 1997 in Jackpot, Ewan, and Paddy bays along Dangerous Passage, and in Herring Bay and surrounding areas on northern Knight Island. In 1998, otters were captured at Herring Bay, Eleanor Island, Esther Passage, Unakwik Inlet, Wells Bay, and Naked Island (Fig.

3.1). Detailed descriptions of the study sites are provided in Ben-David et al. (1998) and Bowyer et al. (1995).

Live capture of otters

We captured 111 individual river otters (Table 3.1), from May through July in 1996 and 1997, and from mid-April through May in 1998, with No. 11 Sleepy Creek® double-jaw leg-hold traps or with Hancock traps (Blundell et al. 1999). Otters were anesthetized with Telazol® (9 mg/kg) administered by Telinject® darts with a blowgun, or by hand injection for otters captured in Hancock traps. Blood samples (7 ml) were drawn from the jugular vein of each otter for DNA analysis. All methods used in this research were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks and adhere to guidelines for animal care and use adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998). Further details on capture and handling are provided in Blundell et al. (1999) and Blundell et al. (2000).

Radiotelemetry

Fifty-five otters were surgically implanted with radiotransmitters (Blundell et al., 2000). Otters receiving transmitters were captured in the vicinities of Jackpot Bay in 1996 and 1997, Herring Bay in 1997 and 1998, and at Eleanor Island in 1998 (Fig. 3.1). Otters were radiotracked, mostly from a fixed-wing aircraft from 1996 through 1999 at Jackpot Bay, from 1997 through 1999 at Herring Bay, and from 1998 to 1999 at Eleanor Island (n = 2,230 total locations). Tracking occurred year-round, but locations were obtained with greater intensity during the mating season (every 4 days), and in summer (every 5-7

days) when weather was more conducive to regular flights. Further details on radiotracking are provided in Blundell et al. (2000, 2001).

DNA Laboratory Procedures

DNA was extracted from frozen blood samples from 110 individual otters with a modification of a protocol described by Groves and Shields (1997). Nine microsatellite loci were screened for this study. These included seven tetranucleotide markers (701, 715, 733, 782, 801, 818 and 829) developed for Eurasian otters (*Lutra lutra*; Dallas and Piertney 1998; and J. F. Dallas, personal communication) and two dinucleotide markers (Mvis075 and Mer022) developed for mink (*Mustela vison*) and ermine (*Mustela erminea*; Fleming et al. 1999). All markers resulted in individual microsatellite fingerprints for each of the river otters evaluated. Amplifications of microsatellites followed protocols described in Blundell et al. (*in review*). Data were sized in base pairs and analyzed with ABI GeneScan 3.1 and Genotyper 2.1 software (Applied Biosystems, Foster City, CA).

Data Analysis

Genetic Differentiation Between Study Areas

We tested for linkage disequilibrium with GENEPOP (Raymond & Rousset 1995*a*) software. Data assessing genetic parameters for populations (e.g., average heterozygosity) were obtained with Biosys-1 (Swofford & Selander 1989). Weir and Cockerham (1984) *F* statistics were calculated with GENEPOP (Raymond & Rousset 1995*a*), including a test for departure from Hardy-Weinberg equilibrium. FSTAT (Goudet 2000) was used to conduct tests of population differentiation not assuming

Hardy-Weinberg equilibrium. For those analyses, genotypic and allelic frequencies were randomized among samples and *G*-statistics (log-likelihood) were calculated (Goudet 2000), adjusting significance levels with sequential Bonferroni corrections (Rice 1989). RstCALC (Goodman 1997) was used to calculate standardized R_{ST}, which corrects for variance among loci and sample sizes among populations.

As a measure of how sociality might affect potential inbreeding within a population, we compared the association between average sociality of otters in a population and F_{IS} value for that population for sites with radiotagged animals (Herring and Jackpot bays, and Eleanor Island). Average sociality was calculated by determining the percentage of telemetry locations each year in which an otter occurred with at least one other otter (Blundell et al. *in press a*) and determining the mean of social locations among all years of telemetry data for each otter. A sample mean was then calculated for mean proportion of social locations among otters for each area.

To examine effects of sample size on estimates of genetic differentiation between populations, we conducted a separate analysis to determine *F* statistics for Herring and Jackpot bays, each with >30 individuals. As a measure of effects of social groups within a population on the genetic structure of populations, we also calculated *F* statistics for individual social groups. The structure of social groups was dynamic (i.e., the same individuals did not occur consistently in the same social groups; Blundell et al. *in review*); thus, the same individual was included in numerous social groups, and group size ranged from two to eight individuals. Because of pseudo-replication, we assessed *F* statistics for 35 social groups solely for the purpose of evaluating heterozygote deficits

within social groups compared with those statistics for each study area. Likewise, we tested for departure from Hardy-Weinberg equilibrium (Ha: heterozygote deficit) among social groups.

To further assess population differentiation, we used multidimensional scaling based on Euclidean distances between allele frequencies of populations (Proxscal; Busing et al. 1997). We also constructed minimum spanning trees from minimum spanning networks calculated for standardized R_{ST} and F_{ST} values with MINSPNET (Excoffier 1993).

Relatedness by Gender and Study Area

Analyses were conducted to test whether mean relatedness of females to females, females to males, and males to males within and between areas was significantly different from random. Juveniles were not included in the analyses to eliminate relatedness of parent-offspring dyads prior to dispersal of offspring, which could potentially mask the effects of sex-biased dispersal. A total of 1,000 randomizations, comparing the mean coefficient of relatedness (R; Kinship – Goodnight et al. 1994) between dyads, were conducted to simultaneously evaluate relatedness within and between areas, keeping group and sex composition constant (i.e., only R values between dyads were randomized). The randomization code for that analysis was written in QuickBasic by E. Geffen.

Each set of gender analyses was conducted twice. The first analyses compared between and within the two areas for which we had telemetry data and the most genetic data (Herring Bay $n = 39$, and Jackpot Bay $n = 31$). A second set of analyses was conducted on all samples collected in 1998, when samples from the other five areas were

obtained and included samples obtained from Herring Bay in that year (seven males, one female). A separate analysis was performed because our sampling design and sample sizes differed among years, and otters in four of those study areas were not radiotracked. At each site in 1998, trapping occurred for only 5 calendar days; thus otters captured may represent individuals most vulnerable to capture. Sample sizes obtained that year ranged from five to 10 individuals per study area (Table 3.1).

Isolation by Distance

We applied Mantel's test (Permute! V. 3.4, Alpha 8; Casgrain 2000) to assess correlation between genetic and geographic distances for all otters in all study areas, and in separate analyses for males and females. Genetic distances assessed were F_{ST}, standardized R_{ST}, Nei's unbiased genetic distance (Nei 1978), the genotype likelihood ratio distance (D_{LR}; Paetkau et al. 1997), and a measure of fuzzy set similarity (D_{fs}; Dubios and Prade 1980), the latter of which was calculated as 1- D_{fs} with Microsat software (Minch 1999). D_{fs} calculates the proportion of shared alleles divided by the proportion of unique alleles among each pair of study areas (Dubios and Prade 1980).

We calculated geographic distances by measuring linear distance between the midpoints (i.e., center) of each study area. Although this represents an unbiased estimate of geographic distance and is therefore useful in comparisons of genetic versus geographic distance, it is not representative of how an otter likely would travel between study areas, because otters generally swim, limiting overland crossings to short distances (Blundell et al. 2001, *in press a*). Accordingly we also compared genetic distances with "otter distances" in a manner similar to that used by Dallas et al. (1999) for *Lutra lutra.*

Otter distance measured a linear course parallel with the shore, incorporating the shortest over-water crossing between landmasses (e.g., across the mouth of a bay, the shortest distance between islands) in the most direct route possible between midpoints of study areas. Measures of geographic distances were obtained with ARCINFO (ESRI, Redlands, California).

Assignment Tests and Dispersal Distances

We used the Bayesian method for assignment tests (GENE CLASS; Cornuet et al. 1999) to detect immigrants into each area. Assignment tests result in assignment of each individual to a study area based upon highest probability, even though the reference areas may not include the true area of origin for an individual. To reduce the potential for assigning otters to unlikely areas, we eliminated individuals from subsequent analyses that had an assignment probability that was less than by chance (i.e., 100/7 study areas = 14.3% probability). We used simulations to assign all otters to a study area from which it originated; simulating multilocus genotypes for 10,000 individuals by randomly sampling alleles according to their frequencies in the samples (Cornuet et al. 1999). After eliminating otters with assignment probabilities of ≤ 0.143, we conducted chi-square analysis to compare the proportion of males and females that were misassigned or correctly assigned to the area in which they were captured (i.e., source study area). We also performed Kruskal-Wallis tests to determine whether assignment probability differed between genders or study areas.

We evaluated dispersal distances with assignment tests by assessing misassigned individuals (i.e., individuals not assigned to the area in which they were captured). For

those individuals, we estimated dispersal distances as distance between the study area in which they were captured and the site to which they were assigned.

Radiotelemetry and Dispersal

We used telemetry data to estimate the probability and characteristics of dispersal for each gender, as well as noting dispersal distances with telemetry observations. Dispersal constitutes the movement of an animal from its place of birth to where it reproduces (Caughley 1977; Shields 1987) and does not involve movements within home ranges, or migration (i.e., between winter and summer ranges; Caughley 1977). To assess natal dispersal, we evaluated movements of young otters that left the area in which they were captured. To assess movement between breeding sites (i.e., breeding dispersal; Greenwood 1980; Shields 1987), we performed multi-response permutation procedure analyses with BLOSSOM software (Slauson et al. 1994), comparing the use of spatial locations for adult male otters during the mating season with those for the remainder of the year. An exact test was conducted for each year of data, comparing the spatial distribution of Universal Transverse Mercator (UTM) coordinates for each male otter from 15 April to 31 May to the distribution of telemetry locations obtained for that male during the rest of the year. Those dates correspond to 2 weeks before the first estrus was detected in female otters in our study areas until 5 days after the last estrus was noted. Herein we report only those patterns of space use that would result in the potential for gene flow during mating season beyond the bay or general area in which an otter was located during the rest of the year.

Migrants Per Generation

We estimated the effective number of migrants (i.e., average number of individuals exchanged) per generation based upon private alleles (Barton and Slatkin 1986) to measure overall immigration into populations. Mean generation time for river otters in Prince William Sound is estimated at approximately 4 years (Bowyer et al. *in review*). We conducted that analysis for all populations with both genders considered together, as well as performing a separate analysis for each gender. When more individuals are sampled per population, a greater number of private alleles are identified, which increases the accuracy of estimates of number of migrants (Slatkin 1985). Therefore, we also assessed private alleles between the two populations for which we had the largest sample sizes (Herring and Jackpot bays; Table 3.1).

RESULTS

Genetic Differentiation Between Study Areas

Genotypes at one locus were independent from genotypes at another locus for each locus pair across all study areas ($p \geq 0.12$, linkage disequilibrium); thus all loci are diagnostic for the purposes of differentiation between sites. Mean heterozygosity among study sites was 43.8% (±0.02 SE) and within sites was >38% (Table 3.1). Mean number of alleles/locus was similar between areas. Study areas with greater sample sizes had higher heterozygosity and lower F_{IS} values (Table 3.1).

Most loci were in Hardy-Weinberg equilibrium in each study area with the exception of two loci at Esther Passage, and one locus each at Naked Island and Unakwik Inlet (Table 3.2). A global test of Hardy-Weinberg equilibrium (Ho: random union of

significant, indicating that otters within sites were more related than expected by chance. In accordance with male-biased dispersal, females in Herring and Jackpot bays were more related to females in their resident area than to males in that area. Additionally, female-female relatedness was greater than male-male relatedness for those areas (Table 3.5), indicating that male dispersal may not occur in sibling groups. Although there was a trend for higher relatedness within than between study areas in 1998, the test was not significant for any gender combination (Table 3.5).

Assignment Tests and Dispersal Distances

Simulations conducted by Cornuet et al. (1999) determined that assignment tests performed well when F_{ST} values were >0.05, and Bayesian assignment was most accurate. Given a mean F_{ST} of 0.06 among loci in this study (Table 3.4), our Bayesian assignments are reasonable, particularly with the elimination of otters with low assignment probabilities. We did not consider population assignments for 10 males (13.3%) and four females (11.4%) because probability of assignment was below the value equivalent to assignment by chance. Of the remaining 94 animals (Table 3.6), 78.1% of males and 83.3% of females were correctly assigned to the study area in which they were captured (i.e., the source site). There also was no difference among areas (df = 6, $p = 0.66$, Kruskal-Wallis) in probability values ($\bar{x} = 0.60 \pm 0.03$ SE, range 0.17 to 0.999). For those otters correctly assigned, assignment probabilities did not differ between genders (males $\bar{x} = 0.60 \pm 0.04$ SE; females $\bar{x} = 0.56 \pm 0.07$; df = 1, $p = 0.87$, Kruskal-Wallis).

A higher proportion of male otters were misassigned (21.9%) compared with females (16.7%), but the proportion of misassigned (Table 3.7) and correctly assigned

individuals did not differ between genders ($\chi^2 = 0.344$, df = 1, $p = 0.6$). Most misassigned males were assigned to nearby study areas (16-30 km distance; Table 3.7, Fig. 3.4), whereas most of the misassigned females were identified as originating from more distant sites (>60 km; Table 3.7, Fig. 3.4).

Radiotelemetry and Dispersal

Telemetry data for river otters also indicated that males and females had an approximately equal probability of natal dispersal. One of 15 females (6.7%) and three of 40 males (7.5%) that were radiotracked showed movement patterns consistent with natal dispersal. Generally, those otters remained in their area of capture for 3-5 months before initiating exploratory movements beyond their previously established range, after which radio contact with some individuals was lost. One young male spent most of 1 year in transit, traveling 47 km southward before eventually settling in an area 32 km south of its original point of capture. Another young male dispersed from Eleanor Island immediately after capture and traveled 71 km southward in ≤14 days. The otter remained at that location for approximately 4 months before radio contact was lost.

Nine adult males (22.5% of all telemetered male otters) showed patterns of movement during mating season that differed with space use during the rest of the year, and likely were consistent with breeding dispersal (Fig. 3.5). Four otters (44.4% of males exhibiting breeding dispersal) completely shifted locations, crossing substantial bodies of open water (≥6 km; Fig. 3.5) to spend mating season in a different area, after which they returned to their original home ranges. Multi-response permutation procedure (MRPP) analyses noted a significant difference in spatial distribution for mating season compared

with the rest of the year for three of those four otters ($p \leq 0.047$, MRPP). The fourth otter ($p = 0.07$, MRPP) took a brief excursion in February, making an open-water crossing of 6 km, but returned to his customary home range until just prior to mating season, whereupon he returned to that new area until mating season was over. The remaining five otters (55.6% of breeding dispersers) temporarily expanded their ranges beyond the bay in which their home range occurred for the rest of the year (Fig. 3.5). Four of those otters had significant shifts in space use ($p \leq 0.008$, MRPP). One otter, which during mating season traveled approximately 25 km south of his customary home range, did not exhibit a significant shift in spatial distribution ($p = 0.17$, MRPP), likely because only one location was detected outside the normal area (Fig. 3.5).

Isolation by Distance

When data from both genders were analyzed collectively, there was a significant positive correlation (Table 3.8) between most measures of genetic distance (except D_{LR} and D_{fs}) and both measures of geographical distance (linear distance and otter distance). A separate analysis by gender noted significant positive correlation between all measures of genetic and geographic distances for males (Table 3.8; Fig. 3.6), with the exception of D_{fs}. Although distances were still positively correlated for female otters, no test was significant (Table 3.8; Fig. 3.6). Relatively large bodies of open water did not appear to constitute a barrier to dispersal for coastal river otters. With telemetry data, we recorded open-water crossings of approximately 6.5 km, and assignment tests indicated that otters of both sexes crossed bodies of water in which the shortest open-water distance was approximately 13 km.

Migrants per Generation

The corrected estimate of the effective number of migrants per generation based on private alleles (Barton and Slatkin 1986) for all otters (both genders) was 6.68 migrants (frequency of private alleles $\bar{x} = 0.035$, mean size of population = 16.7). For male otters, effective number of migrants was estimated at 7.28 individuals per generation (frequency of private alleles $\bar{x} = 0.041$, mean size of population = 10.7) and for females, 1.46 migrants (frequency of private alleles $\bar{x} = 0.123$, mean size of population = 5.7). The estimate for both sexes in Herring and Jackpot bays was 4.49 migrants (frequency of private alleles $\bar{x} = 0.027$, mean size of population = 35). For male otters in Herring and Jackpot bays, 3.88 migrants were identified (frequency of private alleles $\bar{x} = 0.038$, mean size of population = 22.5), and for females, 0.9 migrants (frequency of private alleles $\bar{x} = 0.11$, mean size of population = 12.5).

DISCUSSION

Various aspects of social structure, in particular mating system, dispersal patterns, and group size, influence the genetic structure of populations (Chesser 1991; de Jong et al. 1994). Results from our tests of linkage disequilibrium, *F* statistics, multidimensional scaling of euclidean distances (Fig. 3.2), and minimum spanning trees (Fig. 3.3) indicate that we sampled genetically distinct subpopulations (Table 3.3) with moderate levels of genetic differentiation among loci and evidence of gene flow among sites. Tests of both allelic and genotypic distributions noted that study sites were significantly different, but sites with smaller sample sizes were not distinguishable from each other with *F* statistics. The mutation process for microsatellite loci is not resolved, and considerable debate exists

in the literature about which measure of genetic differentiation is more appropriate (Slatkin 1995; Goldstein and Pollock 1997). That we established clear differentiation between study areas with multidimensional scaling based upon Euclidean distances and allelic frequencies (Fig. 3.2), as well as with minimum spanning trees of standardized values of R_{ST} and with F_{ST} (Fig. 3.3) indicate that study areas were genetically distinct. Genetic data also would seem to indicate that study areas consisted of discrete populations with gene flow between populations; however, we caution that genetic data for each area may not constitute a sampling of the entire population.

Rates and distances of dispersal are a main factor in geographical differentiation at small spatial scales (Forbes and Hogg 1999). Assignment tests indicated that male and female river otters had an equal probability of natal dispersal (Tables 3.6 and 3.7), although we caution that sample size for females was small. Likewise, our telemetry observations noted similar rates of natal dispersal for both genders, in agreement with results reported by Melquist and Hornocker (1983), in which dispersal of telemetered individuals from the natal area was observed for both male and female river otters in a freshwater environment.

Assignment tests indicated a bimodal distribution to dispersal distances (Fig. 3.4) for coastal river otters. Most males and some females moved only short distances, but when females dispersed, most dispersed to distant study sites. Our tests of isolation by distance yielded results consistent with assignment tests. Male otters showed significant isolation by distance (Fig. 3.6; Table 3.8), likely because dispersing males did not travel far (Fig. 3.4, Table 3.7). In contrast, there was no significant isolation by distance for females (Table 3.8; Fig. 3.6), because dispersing females traveled farther than males (Fig. 3.4,

Table 3.7). Moreover, different dispersal distances between genders are consistent with sociality and spatial relationships that we observed among coastal river otters. In earlier studies, we noted that males were highly social but most females remained solitary (Blundell et al. *in press a*). Solitary females tended to occupy exclusive home ranges, but home ranges of solitary males and groups of males overlapped each other, as well as home ranges of females (Blundell et al. 2000). The high sociality and apparent lack of territoriality among male otters would enable dispersing males to relocate to nearby populations, but dispersing females likely would need to travel greater distances to locate available habitat in which to establish an exclusive home range.

Although natal dispersal was similar between genders, differences in movement patterns and potential for gene flow were detected with telemetry tracking that were indicative of a male-biased dispersal via breeding dispersal. Thirty percent of 40 male otters that were radiotracked showed some form of dispersal. Of that dispersal, 22.5% (9 of 40) occurred through apparent breeding dispersal (Fig. 3.5); however, we cannot assess whether breeding dispersal constituted effective dispersal (i.e., resulted in reproductive success). Some males temporarily shifted to a new area, while others expanded their home ranges during mating season. A range expansion during mating season maintains the potential for reproductive success within the resident area as well as increasing the potential for contributing to gene flow beyond the normal range of movements for an otter outside of mating season (Fig. 3.5). Both forms of breeding dispersal indicate male-biased dispersal, potentially facilitating gene flow to nearby populations.

A comparison of F statistics between genders substantiated male-biased dispersal strategies noted with telemetry observations. Females had higher F_{IS} values than males (Table 3.4), probably because most females did not disperse, thus are more likely to share common ancestors. Females likely had higher F_{IT} values because most females that did disperse, moved farther than males (Fig. 3.4), and some may be moving beyond the spatial scale of our genetic sampling (Fig. 3.1). In contrast, males experienced higher rates of gene flow over short distances via breeding dispersal (Fig. 3.5) and natal dispersal (Fig. 3.4, Table 3.7). Therefore, the potential for common ancestry among males is lower among different individuals within subpopulations (F_{IS}) and across all populations (F_{IT}) in the relatively small geographic scale in which we sampled.

In support of the hypothesis of male-biased dispersal, a greater number of effective migrants per generation were detected with private alleles analyses for males, compared with females. Similarly, for Herring and Jackpot bays, females were more closely related to females within a site than to males (Table 3.5), consistent with a hypothesis of male-biased dispersal. Relatedness among male otters within a study area was considerably lower than relatedness among females, also consistent with male-biased dispersal. That we did not detect significant differences in relatedness values within and between study areas for any gender combination for 1998 (Table 3.5) may be a result of sample size (Table 3.1). An incomplete sampling of gene frequencies from a population would make an accurate assessment of relatedness within that population more difficult. Alternatively, perhaps some areas sampled in 1998 (e.g., islands) support only small resident populations, or may be subject to high population turnover as a result of mortality within a site. Each of those

possibilities might result in a propensity toward transient otters that are more vulnerable to capture. Transient otters, arriving from other areas, would not be more related within areas than expected by chance.

Theoretically, sex-biased dispersal may result in local differences in gene frequencies between genders, and random mating in such a population should result in an excess of heterozygotes (i.e., negative F_{IS} values; Prout 1981). Various factors influencing population structure, however, can cause a departure from Hardy-Weinberg equilibrium; consequently interpretation of a particular value of F_{IS} is difficult (Storz 1999). Indeed, sociality among river otters was positively associated with F_{IS} values. Although study areas with higher sociality had higher F_{IS} values (i.e., heterozygote deficit), F_{IS} values for social groups indicated that inbreeding did not occur within those groups. The extent to which excess heterozygosity occurs is directly proportional to the genetic variance between the philopatric sex and the immigrant sex (Storz 1999). The heterozygote deficit we noted is likely a result of nonrandom mating and low genetic variance between genders when gene flow for males via breeding or natal dispersal occurred from neighboring populations. Our tests of isolation by distance indicated that genetic differentiation among males increased with geographic distance; thus, nearby populations were not greatly differentiated (Fig. 3.6, Table 3.8).

Our data provided evidence for male-biased dispersal among coastal river otters, but not in the manner typical of most mammals (Greenwood 1980). Sociality influenced the genetic structure of populations, and gender differences in sociality and spatial relationships resulted in different dispersal distances. Our study indicated that among

coastal river otters, males had greater potential for contributing to gene flow among close populations via breeding dispersal, but both genders exhibited an equal, low probability of natal dispersal, and females in particular may travel 60-90 km during dispersal (Fig. 3.4; Table 3.7).

Given the susceptibility of otters to effects of environmental pollution, (Mason 1989; Serfass et al. 1993; Larivière and Walton 1998) a local extirpation caused by anthropogenic factors would be difficult to remedy with natural recolonization unless the extirpation occurred on a relatively small spatial scale. Assuming that the cause (i.e., source of pollution) was removed, females would eventually immigrate into a vacated area. Generally, fecundity in female mustelids is reduced as a result of exposure to pollutants (Moore et al. 1999; Bleavins et al. 1980), but males are less affected (Bleavins et al. 1980). Therefore, immigrating females potentially could originate from an area beyond the scale of environmental effect, and male otters likely would immigrate from neighboring areas into an unoccupied zone via both breeding and natal dispersal. Although male otters could arrive relatively rapidly, immigration of females would be delayed as a result of low rates of natal dispersal. Our data indicate that natural recolonization of coastal river otters following local extirpation would be a slow process and may be unlikely unless viable populations were available nearby (i.e., within approximately 60 km; Fig. 3.4, Table 3.7). Further exploration of the potential for recolonization among otters is recommended via development of a quantitative spatial model incorporating gender biases in dispersal as well as additional factors such as the

effects of habitat saturation and delayed implantation on dispersal and gene flow, respectively.

Studies such as ours are useful for establishing the geographical scale for contemporary and historical patterns of gene flow (Avise 1994; Forbes and Hogg 1999). Although Prince William Sound was subject to a catastrophic oil spill in 1989, a companion study (Bowyer et al. *in review*) conducted concurrent with this study, 6-8 years after the spill, indicated that river otters were no longer experiencing injurious effects from that spill. Indeed, probability of dispersal and distances dispersed did not differ among otters residing in previously oiled and nonoiled areas (Blundell unpublished data), indicating that otters in all our study areas were experiencing similar population dynamics. Therefore, these data may be useful for modeling exercises to establish the appropriate size of conservation units, as well as determining geographical distances for source populations for translocation to avoid the potential for outbreeding depression or disruption of local adaptations (Hedrick and Miller 1992; Frankham 1995; Forbes and Hogg 1999). Species with evidence of high gene flow among populations may be more appropriate for consideration for translocations (Forbes and Hogg 1999). Because of the isolation by distance that we noted for male otters and limited gene flow for females, we recommend that translocation of river otters should be undertaken with extreme caution to avoid loss of genetic diversity within the species.

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Table 3.1. Genetic diversity for river otters captured in Prince William Sound, Alaska, USA, from 1996 to 1998.

Population	Males (*n*)	Females (*n*)	Mean (SE) Heterozygosity	HWE (SE) expected[a]	Mean (SE)[b] alleles/locus	F_{IS}
Eleanor Island (EI)	7	2	0.383 (0.056)	0.542 (0.055)	3.2 (0.3)	0.306
Esther Passage (EP)	8	2	0.396 (0.073)	0.522 (0.038)	3.1 (0.4)	0.251
Herring Bay (HB)	25	14	0.510 (0.054)	0.553 (0.057)	4.4 (0.5)	0.079
Jackpot Bay (JP)	20	11	0.484 (0.073)	0.512 (0.071)	4.4 (0.7)	0.055
Naked Island (NI)	6	2	0.444 (0.089)	0.504 (0.054)	3.2 (0.4)	0.125
Unakwik Inlet (UI)	4	1	0.444 (0.087)	0.553 (0.056)	3.0 (0.4)	0.216
Wells Bay (WB)	5	3	0.403 (0.074)	0.521 (0.056)	3.1 (0.3)	0.240

[a] Hardy-Weinberg equilibrium; unbiased estimate (Nei 1978).

[b] Minimum and maximum number of alleles per locus were 2 and 10, respectively.

Table 3.2. A test of Hardy-Weinberg equilibrium (exact probabilities) by locus and population for river otters captured in Prince William Sound, Alaska, from 1996 to 1998.

	LOCUS (*p*-values)								
Population[a]	701	715	733	782	801	818	829	m22	m75
EI	1.0	0.48	0.33	0.33	1.0	0.06	0.23	0.23	0.33
EP	1.0	0.02	0.05	1.0	1.0	1.0	1.0	0.56	0.13
HB	0.32	0.45	0.35	1.0	0.64	0.5	0.52	0.2	0.48
JP	0.08	1.0	0.03	1.0	1.0	0.28	0.11	0.69	0.57
NI	0.21	1.0	1.0	0.02	1.0	1.0	1.0	1.0	0.21
UI	0.33	0.37	1.0	0.95	1.0	0.43	1.0	0.95	0.05
WB	0.24	1.0	0.92	0.37	1.0	0.2	0.49	0.44	0.19

[a] Full names of populations indicated here with abbreviations in Table 3.1.

Table 3.3. Genetic distances (F_{ST}\standardized R_{ST}) between study areas in Prince William Sound, Alaska, USA, for river otters captured from 1996 to 1998.

Area[a]	EI	EP	HB	JP	NI	UI	WB
EI		-0.0021	0.1001	0.0784	-0.0153	-0.0310	0.0389
EP	0.160		0.1212	0.1049	-0.011	-0.0300	0.0063
HB	0.1434	0.1983		0.0539	0.0877	0.0101	0.0865
JP	0.1119	0.1423	-0.0139		0.0910	0.0907	0.1128
NI	0.0029	0.0490	0.1725	0.1359		-0.0385	-0.0235
UI	-0.0246	-0.0019	0.1467	0.0925	-0.0311		-0.0175
WB	0.0347	0.0384	0.1667	0.1289	-0.0302	-0.0190	

[a] Full names of populations indicated with abbreviations here are in Table 3.1.

Table 3.4. A comparison of F statistics by gender for river otters captured in Prince William Sound, Alaska, USA, from 1996 to 1998.

Locus	F_{ST}			F_{IS}			F_{IT}		
	Both[a]	Males	Females	Both[a]	Males	Females	Both[a]	Males	Females
701	0.064	0.037	0.141	0.138	0.130	0.098	0.194	0.162	0.225
715	0.034	0.056	-0.023	0.1687	0.180	0.071	0.197	0.226	0.049
733	0.259	0.261	0.238	0.145	0.144	0.114	0.366	0.368	0.325
782	-0.005	-0.006	0.017	0.166	0.219	0.0410	0.162	0.214	0.058
801	0.031	0.026	0.05	-0.054	-0.085	0.039	-0.022	-0.056	0.086
818	0.069	0.049	0.098	0.109	0.029	0.325	0.171	0.076	0.391
829	0.060	0.032	0.17	0.007	-0.026	0.008	0.067	0.007	0.176
m22	0.045	0.059	-0.01	0.175	0.099	0.363	0.212	0.153	0.357
m75	0.020	-0.04	0.395	0.290	0.139	0.376	0.304	0.105	0.622
All loci	**0.074**	**0.064**	**0.131**	**0.127**	**0.090**	**0.171**	**0.191**	**0.148**	**0.279**

[a] Both genders analyzed together.

Table 3.5. A comparison of the mean coefficient of relatedness (*R* values from Kinship; Goodnight et al. 1994) within and between populations by gender for river otters captured in Prince William Sound, Alaska, USA, from 1996 to 1998.

Area[a]	Year	Gender	Mean within	Mean between	*P*-value
HB vs. JP	1996-1998	F - F	0.1430	-0.0434	<0.001
HB vs. JP	1996-1998	F – M	0.0785	0.0295	<0.001
HB vs. JP	1996-1998	M - M	0.0855	0.0229	0.002
All 7 areas	1998	F - F	0.1844	0.0508	0.15
All 7 areas	1998	F – M	0.09	0.0460	0.12
All 7 areas	1998	M - M	0.0865	0.1	0.63

[a] HB = Herring Bay; JP = Jackpot Bay

Table 3.6. Results from assignment tests by gender for river otters captured in Prince William Sound, Alaska, USA, from 1996 to 1998. Numbers are percent assigned. Otters included in assignment tests are those otters with probability values for assignment that were greater than by chance (>14.3% or 100/7 populations).

Source (%)[a]	Assigned Populations[b]													
	EI %		EP %		HB %		JP %		NI %		UI %		WB %	
Total (81.9)	M	F	M	F	M	F	M	F	M	F	M	F	M	F
EI (62.5)	66.7	50	0	0	16.7	0	0	50	16.7	0	0	0	0	0
EP (77.8)	14.3	0	71.4	100	0	0	14.3	0	0	0	0	0	0	0
HB (85.3)	0	0	4.8	0	81.0	92.3	9.5	7.7	4.8	0	0	0	0	0
JP (80.8)	0	0	0	0	17.6	0	82.4	77.8	5.0	11.1	0	11.1	0	0
NI (83.3)	20	0	0	0	0	0	0	0	80	100	0	0	0	0
UI (80.0)	25.0	0	0	0	0	0	0	0	0	0	75.0	100	0	0
WB (75.0)	0	0	0	0	0	33.3	0	0	20.0	0	0	0	80.0	66.7

[a] Total percent correctly assigned to population where otter was captured.

[b] Full names of populations indicated here with abbreviations are in Table 3.1.

Table 3.7. Probability of assignment and distance from assigned population (i.e., population of origin) to population captured in (i.e., source population) for river otters captured in Prince William Sound, Alaska, from 1996 to 1998. Average distance (± SE) for females was 57.9 km ± 11.8, and for males 34.7 km ± 4.3.

Otter	Gender	Source	Assigned	Distance[a] (km)
EI02	M	0.06	0.44 (NI)	21
EI05	M	0.35	0.50(HB)	17.8
EP05	M	0.29	0.58 (JP)	79
EP06	M	0.56	0.62 (EI)	36.9
HB07	M	0.81	0.90 (JP)	28.7
HB11	M	0.29	0.31 (NI)	35.9
HB28	M	0.22	0.48 (JP)	28.7
HB37	M	0.27	0.66 (EP)	54.5
JP10	M	0.11	0.46 (HB)	28.7
JP11	M	0.44	0.72 (HB)	28.7
JP12	M	0.94	0.99 (HB)	28.7
NI07	M	0.89	0.98 (EI)	21
UI05	M	0.62	0.99 (EI)	47.1
WB04	M	0.67	0.82 (NI)	28.7
EI06	F	0.13	0.17 (JP)	38.3
HB13	F	0.29	0.40 (JP)	28.7
JP21	F	0.48	0.98 (UI)	96.6
JP22	F	0.63	0.82 (NI)	62.4
WB03	F	0.06	0.52 (HB)	63.3

[a] Otter distance, measured as the most likely route taken by an otter between areas (linear distance along shorelines and shortest open-water crossings).

Table 3.8. Correlation coefficients (and *p*-values in parenthesis) based on mantel tests between genetic and geographic distances for river otters captured in Prince William Sound, Alaska, USA, from 1996 to 1998.

	All Otters		Males		Females	
Genetic Distance	Otter[a] Distance	Linear Distance	Otter Distance	Linear Distance	Otter Distance	Linear Distance
F_{ST} *r*	0.578	0.577	0.533	0.585	0.387	0.311
(*p*)	(0.005)	(0.003)	(0.009)	(0.004)	(0.19)	(0.273)
R_{ST}[b] *r*	0.502	0.490	0.543	0.582	0.14	0.108
(*p*)	(0.023)	(0.03)	(0.016)	(0.008)	(0.647)	(0.719)
Nei's[c] *r*	0.561	0.55	0.512	0.54	0.286	0.241
(*p*)	(0.006)	(0.006)	(0.024)	(0.006)	(0.344)	(0.431)
D_{LR}[d] *r*	0.364	0.406	0.457	0.509	0.359	0.301
(*p*)	(0.106)	(0.052)	(0.036)	(0.012)	(0.214)	(0.277)
D_{fs}[e] *r*	0.473	0.401	0.484	0.353	0.233	0.224
(*p*)	(0.045)	(0.073)	(0.02)	(0.102)	(0.434)	(0.415)

[a] Otter distances were estimated by calculating the most direct route between study areas in which open-water crossings were measured between the closest possible landmasses.

[b] Standardized R_{ST} (Goodman 1997).

[c] Nei's Unbiased Distance (Nei 1978).

[d] Genotype likelihood ratio distance (Paetkau 1997).

[e] Fuzzy set similarity – proportion of shared alleles divided by proportion of unique alleles (Dubois and Prade 1980).

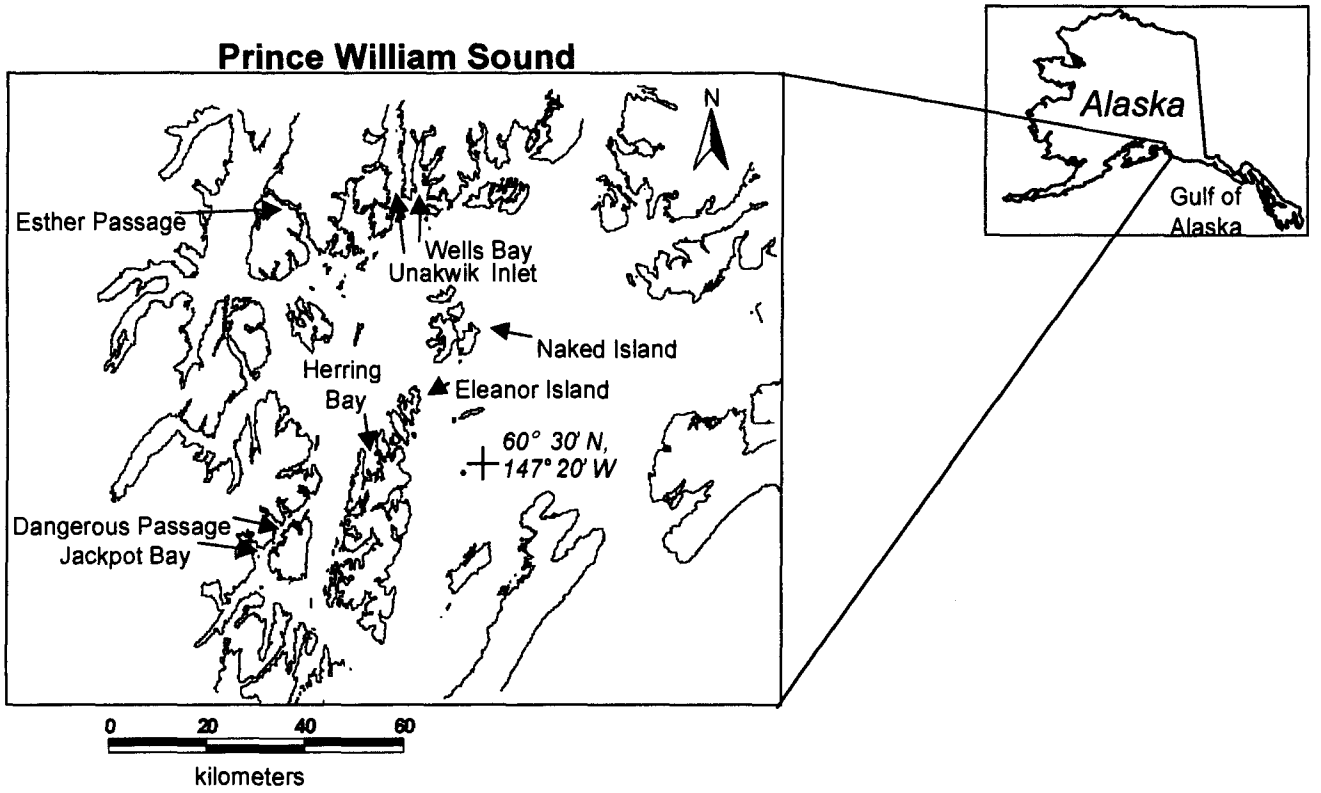

Figure 3.1 - Study areas in Prince William Sound, Alaska, USA. Genetic data (microsatellite DNA) were obtained from river otters ($n = 110$) captured in all study areas (indicated with arrows) from 1996 to 1998. Fifty-five otters were radiotracked in the vicinities of Jackpot Bay, Herring Bay, and Eleanor Island from 1996 to 1999.

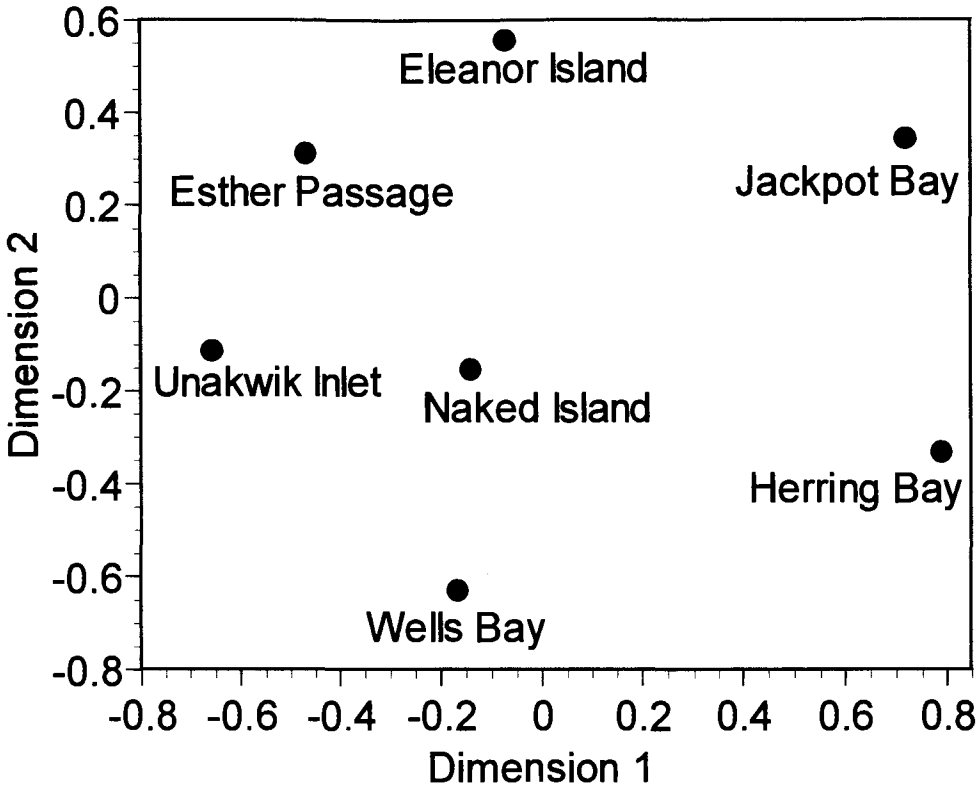

Figure 3.2 - Multidimensional scaling (standardized Euclidean distances) to establish genetic differentiation between populations of river otters based upon allele frequencies from microsatellite DNA. DNA samples were obtained from 110 river otters captured in seven areas in Prince William Sound, Alaska, from 1996 to 1998. Names of study areas are indicated under symbols. Dispersion accounted for in this analysis was 0.9697, normalized raw stress score was 0.030.

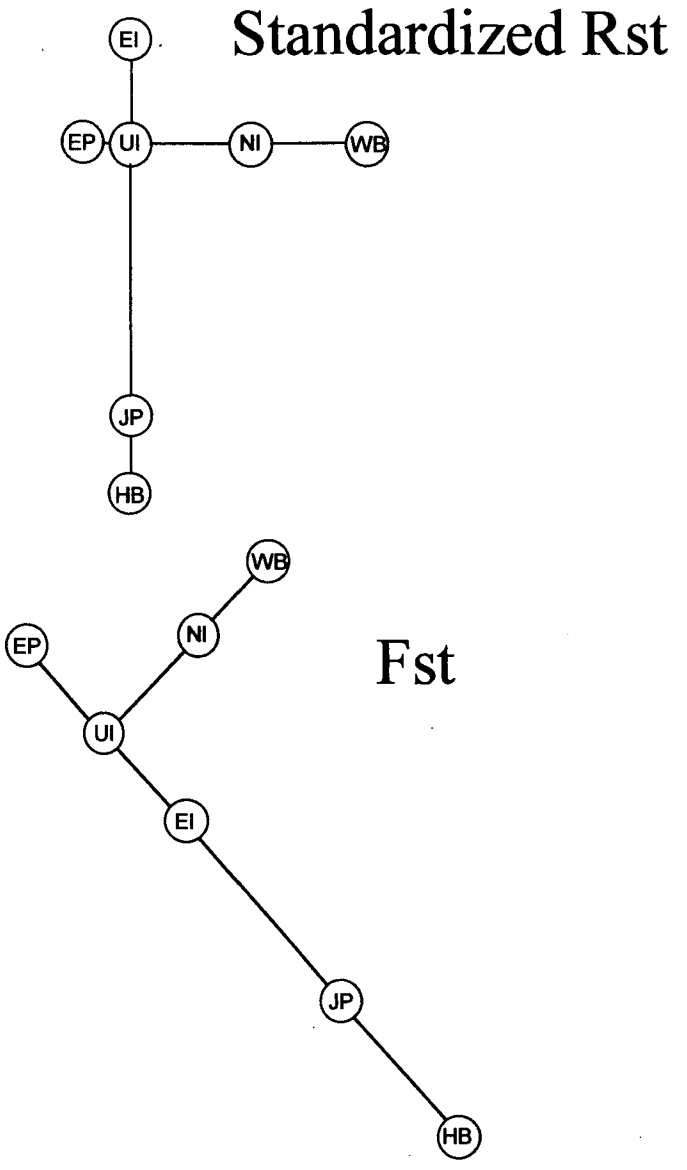

Figure 3.3 - Minimum spanning trees constructed from minimum spanning networks to establish genetic differentiation between populations of river otters based upon genetic distances: standardized Rst (top) and F_{ST} (bottom) from microsatellite DNA. Genetic data were obtained from 110 river otters captured in seven areas in Prince William Sound, Alaska (Fig. 1), from 1996 to 1998. Abbreviations for names of study areas are indicated in circles, full names and abbreviations for study areas are shown in Table 1.

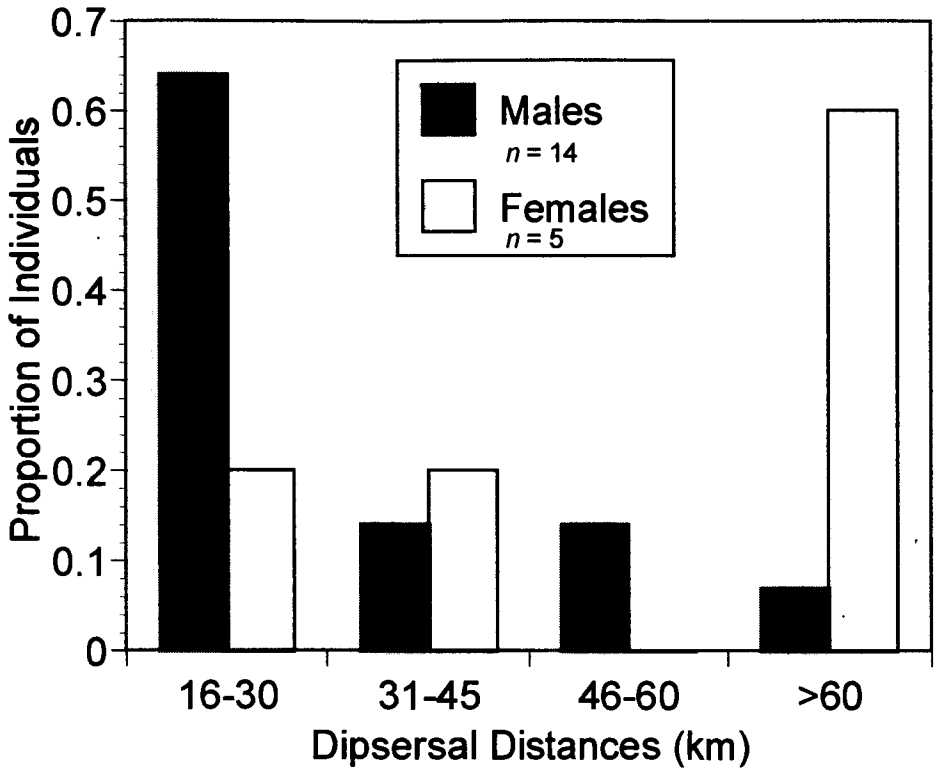

Figure 3.4 - Dispersal distances for river otters captured in Prince William Sound, Alaska. Data are based upon assignment tests and misassigned individuals (i.e., those not assigned to the area in which they were captured). Distances are measured as the most direct swimming route between the area an individual was captured in and the area to which it was assigned for all misassigned individuals that had a probability greater than chance of belonging to the area to which they were assigned.

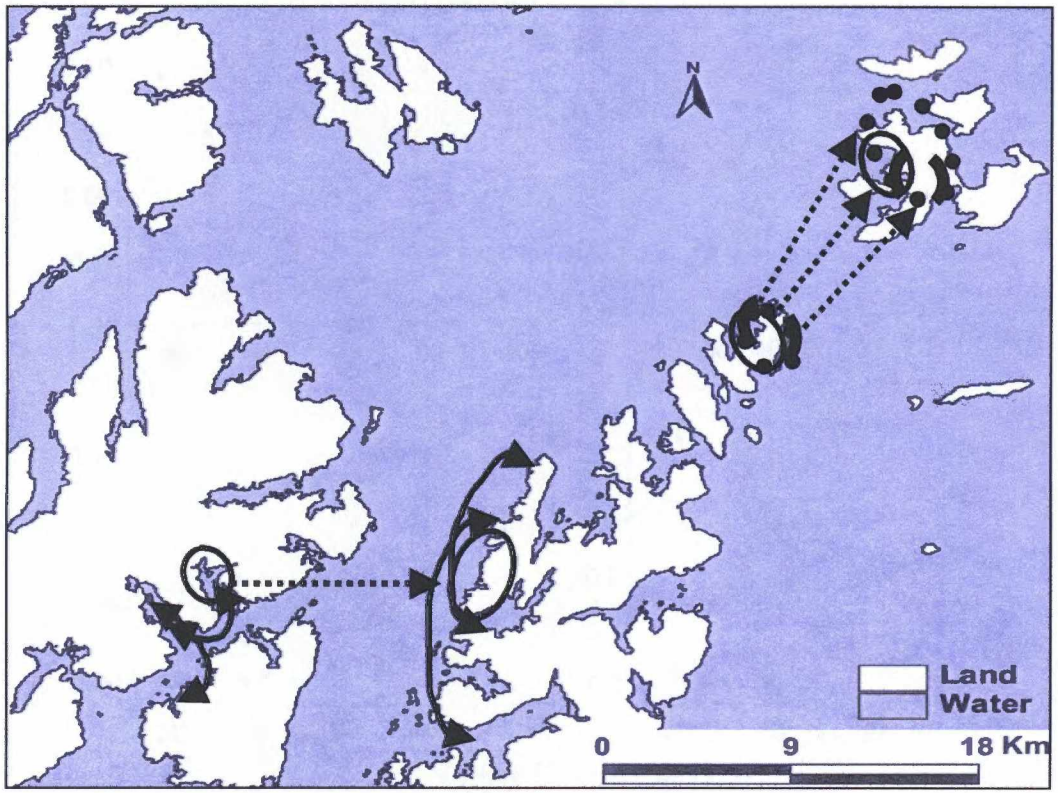

Figure 3.5 - Types of breeding dispersal exhibited by male river otters in Prince William Sound, Alaska, from 1997 to 1999. A total shift in location during the mating season is indicated with two ovals connected by a dotted line; the arrow points to the area associated with locations during the mating season. Solid lines with arrows on both ends indicate an expansion of the area traveled during the mating season, from the midpoint of normal range to the maximum distance traveled during the mating season.

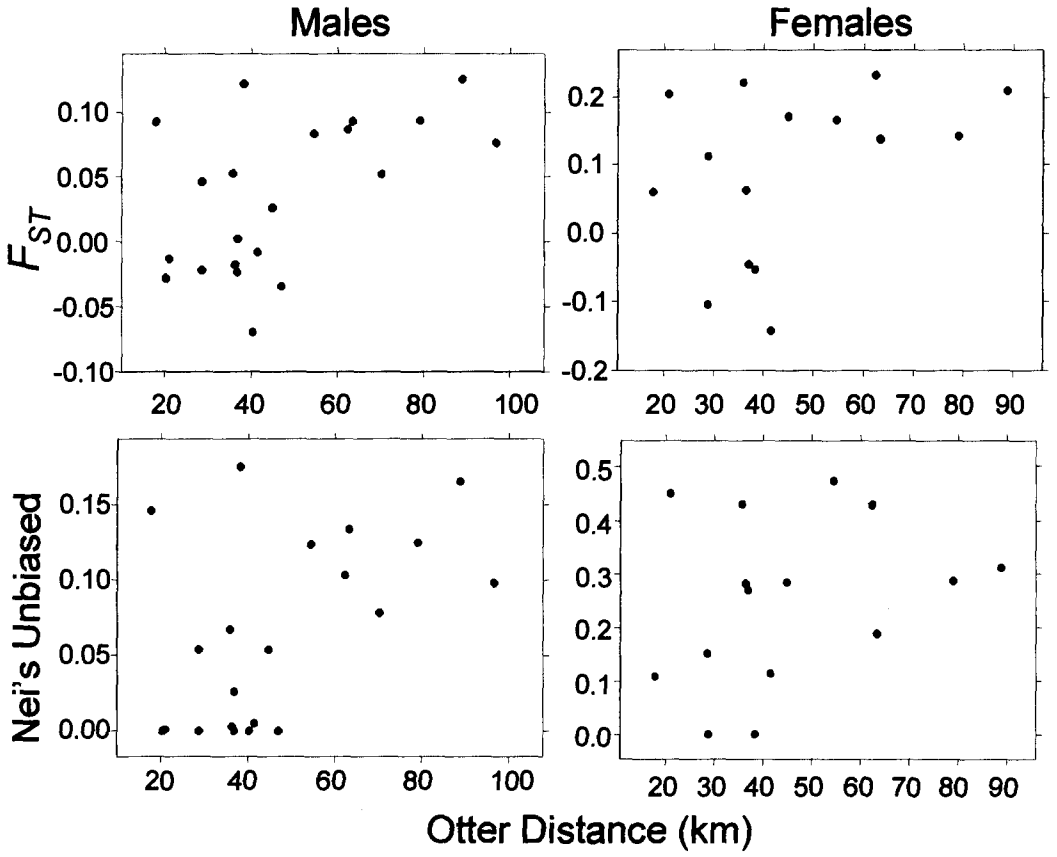

Figure 3.6 - A test of the hypothesis of isolation by distance for male and female river otters in Prince William Sound, Alaska, USA, assessing correlation of geographic and genetic distances. Results were significant for males, but not for females. Distance measures shown here are those that showed lowest *p*-values among the distance measures evaluated (Table 3.8).

CONCLUSIONS

This research investigated form and function of social groups for river otters inhabiting marine environments in Prince William Sound, Alaska, and the role of sex-biased dispersal in establishing patterns of gene flow among populations. At the onset of this study, little was known for this species about the topics included in this dissertation. As with any research, the more that is learned, the more questions that arise. Nonetheless, this study provides considerable insight into social organization and dispersal, and some preliminary insight into the mating system of these secretive mustelids.

This study noted no evidence that association with kin was beneficial, and social groups were not composed of kin. Neither was there evidence that association with a group had a cost or offered a benefit with respect to reproductive success, nor that reproductive success for male otters was related to secondary sexual characteristics. Although hypotheses of avoidance of predators could not be directly assessed, several lines of evidence indicated that formation of groups likely was not an anti-predation strategy. The weight of evidence indicated that association with a group offered ecological benefits of increased access to a higher-quality prey, likely as a result of cooperative foraging.

Social groups were composed primarily of male otters, leading me to postulate that reproductive females likely were occupied with the time-consuming prospect of raising offspring at a time when association with a group would be most beneficial. In years when females are not raising offspring, however, their best strategy would be to

join male groups to take advantage of the benefits of cooperative foraging and the associated access to better quality prey that are difficult to obtain as a solitary predator. For male otters, timing of availability of high-quality pelagic fishes in the nearshore system does not require a tradeoff between cost and benefit. Therefore male otters can be social when it is beneficial, when high-quality prey are available and more easily obtained via cooperative foraging, and leave the group when sociality would be costly, during competition for reproductive opportunities.

Sociality influenced the genetic structure of populations. The switch for male otters, from social to nonsocial prior to mating season, facilitated a male-biased breeding dispersal that contributed to gene flow among nearby populations of coastal river otters. Both genders exhibited low rates of natal dispersal, but data from assignment tests indicated a bimodal distribution to dispersal distances, likely explained by gender differences in sociality and spatial relationships. Because female otters tend to be solitary and occupy exclusive home ranges, when a female chooses to disperse, likely she would need to travel further to find an unoccupied area. The more gregarious nature of male otters, however, would permit a male to travel only a short distance before encountering a new area and group with which to socialize. Accordingly, among coastal river otters, males had greater potential for contributing to gene flow among close populations via breeding dispersal, but both genders exhibited an equal, low probability of natal dispersal, and females in particular may travel 60-90 km during dispersal.

Recovery from a local extirpation via natural recolonization would therefore be a slow process because of different dispersal strategies and distances for each gender.

Although males may arrive from nearby populations relatively rapidly via both breeding and natal dispersal, recolonization by females would be a slow process as a result of the low rates of natal dispersal. This research indicated that natural recolonization of coastal river otters following local extirpation is unlikely unless viable populations were available within approximately 60 km. Translocation of otters, however, should be undertaken with extreme caution. Populations of coastal river otters are genetically distinct as a result of sex-biased dispersal. The combination of isolation by distance for male otters and low gene flow for females accentuates genetic differentiation among populations; thus selection of stock for reintroduction should be conducted with care to avoid outbreeding depression and to preserve genetic diversity in the species

Various aspects of social structure, in particular mating system, dispersal patterns, and group size, influence the genetic structure of a population. This research provided insights into gender differences in social organization, dispersal strategies, and gene flow among populations of coastal river otters. Unquestionably, there are factors that define social organization and the mating system among these otters that have not been identified. If sociality results in a better quality diet and does not have a cost to males in terms of reproductive success, and if timing of prey availability permits males to switch from social to nonsocial when competition for reproductive opportunities would be high; it would seem that all males should be social outside of mating season. Why some males remain solitary is a mystery. Long-term studies are therefore recommended to elucidate the mating system among coastal river otters.

Many studies fail to consider that different ecological and reproductive constraints may differentially affect the genders. Throughout this research, data were analyzed considering genders together and independently. In most cases, analyses by gender yielded different results. For example, a significant test of isolation by distance for both genders combined, indicated that geographic distance serves as a barrier to dispersal for coastal river otters. That pattern held true for male otters, evaluated independently, but when females were analyzed separately, there was no support for that hypothesis. As was substantiated by data from assignment tests, when females disperse, they travel further than males. Different dispersal distances between genders of coastal river otters indicate that the spatial scale of a conservation unit for female otters differs from that of males. Results from this and other studies investigating differences between genders indicate that implementation of management for any species should give consideration to gender differences before policy decisions are made. In many instances it may be that each gender may need to be managed separately

APPENDIX 1

RH: Live Trapping of River Otters•Blundell et al.

Capturing river otters: a comparison of Hancock and leg-hold traps[1]

Gail M. Blundell, John W. Kern, R. Terry Bowyer and Lawrence K. Duffy

Abstract We tested the efficiency of Hancock and #11 leg-hold traps (Sleepy Creek®) for live capturing river otters (Lutra canadensis) in Prince William Sound, Alaska, during spring-summer 1996. We captured 39 individual otters 46 times (25 males and 14 females). Efficiency of capture did not differ significantly ($P > 0.13$) between trap types whether we used trap nights or latrine sites as sampling units. We captured (1 otter/26.5 trap nights) in Hancock and (1 otter/21 trap nights) in leg-hold traps. Rate of malfunction between types of traps also was similar ($P > 0.50$), but leg-hold traps were easier to transport and had significantly ($P = 0.03$) greater utility. Although there was no significant difference in the trauma to otters captured by Hancock or leg-hold traps ($P > 0.60$), the nature of injuries to otters differed between the types of traps ($P < 0.05$): Hancock traps resulted in significantly ($P = 0.003$) more injuries to teeth. We recommend the use of the leg-hold

[1] Blundell, G. M., J. W. Kern, R. T. Bowyer, and L. K. Duffy. 1999. Capturing river otters: a comparison of Hancock and leg-hold traps. Wildlife Society Bulletin 27: 184-192.

trap because otters recovered from injuries to appendages, but damage to teeth of adult otters is permanent.

Key words Alaska, capture, efficiency, Hancock trap, injury, leg-hold trap, Lutra canadensis, river otter, teeth, trapping

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Introduction

The ability to live capture study animals is an essential component of many research and management programs (Schemnitz 1994). Both Hancock and leg-hold traps have been used to live capture river otters (Lutra canadensis) with varying degrees of success. For instance, the number of trap nights required to capture a river otter in a Hancock trap ranged from 58 to 123 nights (Melquist and Hornocker 1983, Shirley et al. 1983, Woolington 1984). Likewise, rates of captures for various types of leg-hold traps ranged from 60-315 trap nights/otter captured (Shirley et al. 1983, Serfass et al. 1996).

Other potential differences between Hancock and leg-hold traps have been reported in the literature. Use of Softcatch® leg-hold traps resulted in a high rate of escape (43% of 51 potential captures; Serfass et al. 1996); modifications of the Hancock trap are thought to make it more efficient (Northcott and Slade 1976). The cumbersome size of Hancock live traps (95 by 59 by 40 cm; > 11 kg), however, may limit the number of traps that can be transported efficiently or the locations or size of areas in which these traps can be set appropriately. Moreover, river otters may learn to avoid capture in Hancock traps (Duffy et al. 1994a).

Few data are available on injuries to river otters resulting from the methods used to capture these large mustelids. Shirley et al. (1983) reported 16% of 30 river otters experienced a broken toe from being captured with an unpadded leg-hold trap, but most otters had only minor skin lacerations or suffered no injury. Serfass et al. (1996) compared injuries to otters from Softcatch® leg-hold traps and traps without padded jaws. Traps with padded jaws caused injury rates of 38% for canine teeth and 38% for appendages (n = 29 otters). Private trappers using unpadded traps caused much greater injuries to otters, but the types of traps and handling techniques varied markedly (Serfass et al. 1996). The efficiency of traps in capturing terrestrial carnivores and the injuries caused from these traps was reviewed by Hurbert et al. (1996). No study has evaluated injuries caused to otters by Hancock traps.

We evaluated the capture success and injury rate for river otters live captured in Hancock and unpadded leg-hold traps. Specifically, we tested for differences in capture efficiency, rate of escape, rate of malfunction, and utility of these types of traps.

Additionally, we tested for differences in severity and types of injuries to otters from Hancock and leg-hold traps.

Study area

We conducted research on river otters in two areas of Prince William Sound, Alaska, from late April to August 1996. One area included Herring Bay and surrounding areas (45 km of shoreline) on northern Knight Island (60º30'N, 147º40'W). The second study site encompassed Jackpot, Ewan, Paddy bays (55 km of shoreline) along Dangerous Passage (60º20'N, 148º10'W); the study sites are located 30 km apart. Both locations are typical of coastal areas in Prince William Sound and are composed of rocky and often steep shorelines with many bays and inlets.

The Sound has a cool maritime climate and receives approximately 200 cm of annual precipitation and > 100 cm of snowpack; snow often persists along the shorelines until late April or earlly May. Dense, old-growth forest characterized by hemlock (Tsuga sp.) and Sitka spruce (Picea sitchensis) is typical at lower elevations with alpine tundra occurring at higher elevations. Muskegs occasionally are interspersed with old-growth forest.

River otters in Prince William Sound occur at densities of 28-80 animals/100 km of shoreline (Testa et al. 1994), with home ranges that encompass about 20-40 km of shoreline (Bowyer et al. 1995). These otter forage extensively in intertidal and subtidal zones where they prey principally on marine fishes (Bowyer et al. 1994). River otters living in this marine environment form large social groups ($\leq$ 13 individuals), which congregate at latrine sites (Rock et al. 1994). Otters exhibit habitat preferences for

latrines (Bowyer et al. 1995), which helped us locate these areas for the live trapping of otters.

Methods

We live captured river otters at latrine sites (Testa et al. 1994, Bowyer et al. 1995) from May to August 1996, but most trapping effort was concentrated in May and June. We set either Hancock or #11 (Sleepy Creek®)double-jaw leg-hold traps with long springs (Fig. A.1.1) at appropriate locations depending on topography, substrate, and width of otter trails at latrines. The Sleepy Creek® trap is sufficiently small that it typically does not reach and break long bones, yet applies sufficient force to the foot to hold most otters. Additionally, we varied the number and type of trap set based on the size of the latrine site, which typically extend 5-20 m across.

All traps were set on land without the use of lure or bait (i.e., blind sets). Leg-hold traps were boiled in a solution of trap wax (Sterling Fur and Tool Co., Sterling, OH), and we used rubber gloves for handling the trap and a rubber pad to kneel upon while making a set. Some leg-hold traps were anchored with 38-cm angle-iron stakes, with double-swivel tips at the top of the stake that allowed the trap to rotate 360º around the stake. Additionally, we wired the stake at ground level to a tree root beyond the immediate site of the trap to assure that otters could not uproot stakes when the ground was saturated by rainfall, which occurred regularly in Prince William Sound. If, however, an obstruction at the trip site prevented the trap from rotating 360º, we anchored the trap to that obstruction, provided it was sufficiently strong to hold an otter; otherwise, we removed the obstruction from the site. We kept trap chains short ($\leq$ 70 cm) to reduce the

possibility of entanglement in surrounding vegetation and placed swivels at the point of attachment to the trap, at the anchor point, and at 45-cm intervals along the chain. We dug traps into the substrate so that the top of the jaws were flush with the surface. A small piece of wax paper was placed over the pan of the set trap, and the trap was covered and camouflaged with surrounding dirt or vegetation. Traps were equipped with transmitters (Telonics®, Mesa, AZ) that indicated when they were sprung; we monitored these signals a minimum of 2-3 times each day.

Because of their large size, we soaked Hancock traps in saltwater for 12 h before their initial use, rather than boiling them in a solution of trap wax. We used similar precautions to those we employed for leg-hold traps to avoid contaminating the trap or site with human scent. We buried the set Hancock trap level with the surface and camouflaged it, but the angle of the open trap (120º) required that the topography of the latrine site accommodate the Hancock trap (i.e., provided a solid backing for the upright portion of the trap; Fig. A.1.1). The trap was firmly anchored to a nearby tree, but no swivels were attached because a captured otter was contained with the trap. As before, we monitored such sets regularly with a trap transmitter.

We hand injected otters captured in Hancock traps with Telazol® (9 mg/kg body wt.), and anesthetized otters in leg-hold traps using Telinject® darts (Saugus, CA) with the same dose of Telazol® but delivered with a blow gun (Zoolu Arms, Omaha, NE). The maximum time between when an otter was captured and immobilized ranged from 7 to 11 h, but most were attended within 4-5 h.

We thoroughly inspected each immobilized otter for injuries, especially to teeth or appendages. Old injuries to teeth were typified by discoloration of the broken area, smooth rounded edges at the fracture site or the absence of gum damage when incisors were missing. Likewise, we determined old injuries to appendages from the absence of recent edema, lacerations, luxations, and fractures. We excluded old injuries from our analyses. Each otter was assigned to an age category (adult $\geq$ 2 years, yearling, or young of the year) based on the size of otters, and tooth irruption, wear, and staining. Otters were held in a capture box and released on site after they had completely recovered from anesthesia.

Because we first trapped otters at Herring Bay and then at Jackpot Bay, we confined our analysis of the performance of leg-hold and Hancock traps to Herring Bay to avoid confounding effects of season. Moreover, we trapped otters at Jackpot Bay and vicinity mostly with leg-hold traps because the nature of latrine sites and shorelines was more suitable for those sets; no otters were captured at Jackpot Bay in Hancock traps. We tested for differences in capture between trap types by sex and age class using a 2-sample $\underline{Z}$-test for proportions (Remington and Schork, 1970:217).

Four criteria were used to compare leg-hold and Hancock traps at Herring Bay. We assessed capture efficiency (captures/trap night), trap utility (number of latrines with traps/total number of latrines), escape rate (escapes/escapes + captures), and malfunction rate (traps sprung/trap night). These criteria each measure a different aspect of how the type of trap will influence maintenance of the trap line and trapper effort. Capture efficiency is a relative measure of how much effort is required to catch a specific number

of animals. Escape rate gives a measure of how much effort is required to catch a specific number of animals. Escape rate gives a measure of trap performance, providing an animal springs and escapes from a trap. Malfunction rate provides an indication of the amount of trapping effort required to keep the trap line functioning. Trap utility measures how often a particular type of trap is suitable for a specific location.

Because traps were monitored with telemetry receivers and not examined visually each day, traps potentially could be sprung without triggering the trap transmitter. Due to the force with which a Hancock trap is sprung, all trap transmitters were triggered on this type of trap. On 6 occasions, however, this problem occurred with leg-hold traps. Consequently, we adjusted trap nights for calculations of efficiency and rate of malfunction for leg-hold traps. Thus, on 5 of 6 occasions, these traps were examined visually every other day, and on 1 occasion on the third day resulting in expected trap nights totaling 11 (i.e., $6 \cdot 1.5 + 1 \cdot 2 = 11$ adjusted trap nights). These same occasions represented 15 uncorrected trap nights. We examined differences among measures of trap performance with a chi-square test (Fleiss, 1981). We also used logistic regression (Agresti 1990) to evaluate trap efficiency using latrine sites and total trap nights as sampling units.

Captures of river otters on both study sites (Herring and Jackpot bays) were used for analysis of trap injuries. Although 6 otters were recaptured at least once, we included only injuries sustained in their initial capture in our analysis. Injuries were scored on the basis of a standardized scale of trauma (Table A.1.1). This scale was developed through the International Organization for Standardization of Traps (Olsen et al. 1986, Jotham and

Phillips 1994). Point values were established considering pain, loss of function, severity of wounds, potential for healing, and whether the animal could be released. Although this scale was developed to assess injuries during necropsy examinations, we were able to assess most injuries with gross examinations of otters in the field. We compared rankings of injuries from Hancock and leg-hold traps using this scale with a Wilcoxon rank-sum test (Walpole and Meyers 1989:626); SAS statistical software was employed in this analysis (SAS Institute Inc. 1996).

Results

We live captured a total of 39 individual river otters from out 2 study sites in Prince William Sound: 20 otters from Herring Bay and 19 otters for Jackpot Bay. These animals included 12 adult ($\geq$ 2 yrs) males, 13 yearling males, 8 adult females, 5 yearling females, and 1 young female (3-4 months of age). Overall, 64.1% of 39 otters were male, and 51.3% were adults. For leg-hold traps, 79.3% of 29 otters were captured by a forefoot, the remainder by a hindfoot; Hancock traps contained the otter within the trap. Some otters were captured more than once: 2 adult and 3 yearling males, and 1 yearling female were recaptured once, and 1 adult male was recaptured twice. No otters first captured in Hancock traps were recaptured in this trap, whereas 4 otters were recaptured in leg-hold traps. No difference occurred in the proportion of males live captured in Hancock (70.0% of 10 otters) or leg-hold (62.1% of 29 otters) traps ($\underline{Z} = 0.46$, $\underline{P} > 0.64$). Likewise, the proportion of adult otters we captured did not differ between types of traps (Hancock, 40 % of 10 otters; leg-hold, 55.2% of 29 otters; $\underline{Z} = 0.83$, $\underline{P} > 0.40$). We captured 4 mink (Mustela vision) and 2 porcupines (Erethizon dorsatum) in leg-hold traps;

no animals received serious injuries. No nontarget species were captured in Hancock traps.

We confined our analysis of how Hancock and leg-hold traps functioned to Herring Bay because we captured no otters in Hancock traps at Jackpot Bay in 196 trap nights of effort. Hancock traps had a slightly lower efficiency, a higher escape rate, a lower rate of malfunction, and a much lower utility than did leg-hold traps; however, only utility differed significantly between types of traps (Table A.1.2).

We used two logistic-regression models to further evaluate the efficiency of Hancock and leg-hold traps in capturing river otters. These analyses allowed an evaluation of the effect of having more than one trap or more than one type of trap set at some latrine sites. The first model used latrine sites as sampling units ($\underline{n} = 32$) and total captures at a latrine. (0, 1, 2-3 otters) as the dependent variable. This conservative approach showed no effect of trap type ($\underline{X}^2 = 1.03$, 1 df, $\underline{P} > 0.30$), number of traps at a latrine ($\underline{X}^2 = 0.06$, 1 df, $\underline{P} > 0.80$), number of trap nights ($\underline{X}^2 = 0.35$, 1 df, $\underline{P} > 0.34$), or an interaction between type of trap and number of traps ($\underline{X}^2 = 0.49$, 1 df, $\underline{P} > 0.48$). The second model used trap nights as the sampling unit ($\underline{n} = 526$) and whether an otter was captured in a trip (0,1) as the dependent variable. Again, no effect of trap type ($\underline{X}^2 = 2.22$, 1 df, $\underline{P} > 0.13$), number of traps at a latrine ($\underline{X}^2 = 0.29$, 1 df, $\underline{P} > 0.59$), or their interaction ($\underline{X}^2 = 1.76$, 1 df, $\underline{P} > 0.18$) occurred.

Our analyses of injuries received by otters from their capture were based on first captures in each type of trap. This includes 2 otters that were first captured in one type of trap and then in the other. Consequently, our sample size for this analysis is 41 otters.

Overall, 65.9% of 41 otters received some type of injury associated with being live captured; no difference occurred ($\underline{Z} = 0.90$, $\underline{P} > 0.36$) in the proportion of otters injured by Hancock (54.6% of 11 otters) or leg-hold (70% of 30 otters) traps. Similarly, the type of trap did not disproportionately injure the sexes of otters. For Hancock traps, 83.3% of 6 injured otters were male, whereas for leg-hold traps 66.7% of 21 injured otters were male ($\underline{Z} = 0.90$, $\underline{P} > 0.36$). Adult otters were injured at a lower rate (and hence other age classes were injured more often) in Hancock (18.2% of 11 otters) compared with leg-hold (40.4% of 30 otters) traps; this difference, however, was not significant ($\underline{Z} = 1.49$, $\underline{P} > 0.13$). This analysis combined both serious and minor injuries; consequently, we further evaluated how severely otters were injured using the scale in Table A.1.1.

Trauma scores (Table A.1.1) for river otters captured in Hancock traps ($\underline{n} = 11$) ranged from 0 to 95 with a median of 20 points (higher scores reflect more serious injuries). These scores for leg-hold traps ($\underline{n} = 30$ otters) ranged from 0 to 100 with a median of 5 points. A Wilcoxon rank-sum test indicated no significant difference in injuries to otters caused by the type of trap used to capture these mustelids ($\underline{P} > 0.60$).

The trauma scale addresses the overall seriousness of injury to otters, but does not adequately evaluate the disparate type of injuries caused by Hancock and leg-hold traps because of the way these traps capture and restrain otters. To quantify the nature of such injuries, we subdivided the types of trauma caused by live traps into those associated with damage to teeth or appendages (all injuries to otters could be placed in these categories). Hancock traps exhibited a marginally nonsignificant ($\underline{Z} = 1.953$, $\underline{P} = 0.051$) propensity to injure both appendages and teeth (36.4% of 11 otters) more often than did leg-hold traps

(6.7% of 30 otters). The injuries to appendages incurred by otters captured in Hancock traps, however, were confined to edema and abrasions.

To meet assumptions of the chi-square analyses, we partitioned the seriousness of injuries into 2 categories: none to minor injuries (0-15 on the trauma scale); and serious injuries (25-100 on the trauma scale; Table A.1.1). This categorization was based on our experience with the outcomes from injuries otters received from the live traps. When severity and type of injury were considered, otters captured in Hancock traps had significantly more serious injuries to their teeth than for animals captured in leg-hold traps (Fig. A.1.2). Although more serious injuries to appendages resulted from their capture in leg-hold compared with Hancock traps, this difference was not significant (Fig. A.1.2).

Because injury to teeth differed by type of trap, we further partitioned these data according to which teeth were damaged. We documented no injury to incisors, but observed fractures of both molariform and canine teeth. Hancock traps were significantly more likely to cause injury to both types of teeth, but such injuries were more pronounced among canine teeth (Fig. A.1.3).

Discussion

Hancock traps did not differ from leg-hold traps in most measures of trap function (Table A.1.2). Certainly, the leg-hold trap was lighter, easier to transport and set, and had significantly greater utility (Table A.1.2). We observed no difference in efficiency whether trap nights (Table A.1.2) or latrine sites were used as sampling units, even when we controlled for multiple sets of both types of traps at latrines. We caution, however, that river otters may become trap shy from their capture in Hancock traps (Duffy et al. 1994a).

Indeed, we had no recaptures of river otters in Hancock traps, but 4 otters were recaptured in leg-hold traps.

A comparison of escape rates for the Sleepy Creek® #11 leg-hold trap used in our study (15.4% of 13 otters; Table A.1.2) with the padded-jaw trap employed by Serfass et al. (1996) (43% of 51 otters) indicates a significantly ($Z = 2.27$, $P < 0.03$) lower loss of otters from our traps. Many factors, including how long the animal was in the trap and whether the trap was set on land or in water, might affect the rate at which otters escaped from traps. We believe, however, our methods and the type of trap we used offers a substantial improvement in the number of otters retained in traps. Clearly, a high rate of escape from traps could pose problems where some minimum number of animals was necessary to test hypotheses concerning the behavior, ecology, or physiology of otters (Duffy et al. 1993, 1994b, Testa et al. 1994, Bowyer et al. 1995), or where some minimum number of animals were needed for translocation (Erickson and McCullough 1987, Reading and Clark 1996).

No overall difference occurred in trauma (Table A.1.1) caused by Hancock or leg-hold traps to otters, but this analysis did not consider the disparate type of injuries caused by these traps. Hancock traps were prone to cause serious injuries to teeth, whereas differences in injuries to appendages were similar between Hancock and leg-hold traps (Figs. A.1.2, A.1.3).

Injuries to teeth of otters captured in the padded-jaw trap (37.9% of 29 otters) used by Serfass et al. (1996) also was significantly ($Z = 3.09$, $P < 0.002$) higher than for the unpadded leg-hold trap we used (6.7% of 30 otters); perhaps otters broke teeth on the

steel flange covering the padded jaws. Serious injuries to appendages were similar ($Z = 0.72$, $P > 0.47$) for the padded-jaw trap (10.3% of 29 otters) and the unpadded trap we used (16.7% of 30 otters). Shirley et al. (1983) also reported a rate of serious injuries to appendages from the use of unpadded leg-hold traps (Victor #11 double long spring) identical to ours (16.7% of 30 otters).

We believe that live capture of river otters with the leg-hold trap caused less permanent damage than did Hancock traps. The teeth of carnivores are designed to withstand the forces necessary to capture and consume prey, although some natural breakage of teeth occurs (Van Valkenburgh 1988). Nevertheless, the tooth damage that occurred from Hancock traps (> 45%; Fig. 3) is excessive and was not ameliorated by the limited time that otters spent in traps. Indeed, otters were held longer in leg-hold traps (about 10 h) than in Hancock traps (about 8 h). Damage to canine and molariform teeth in adult otters is permanent and can represent a serious impediment to the capture and mastication of prey (Biknevicius and Van Valkenburgh 1996). Although some serious injuries to appendages are caused by leg-hold traps, such damage often heals with no apparent debilitation (Shirley et al. 1983). Consequently, we recommend the use of the Sleepy Creek® No. 11 leg-hold trap and our methods for the live capture and handling of river otters.

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Table A.1.1. Trauma scale for traps used to assess damage to river otters (from Olsen et al. 1986, Jotham and Phillips 1994).

Pathological Observations	Score (points)
Claw loss	2
Edematous swelling or hemorrhage	5-15
Minor cutaneous laceration	5
Minor subcutaneous soft tissue maceration or erosion	10
Major cutaneous laceration, except on foot pads or tongue	10
Minor periosteal abrasion	10
Severance of minor tendon or ligament	25
Amputation of 1 digit	25
Fracture of a permanent tooth exposing pulp cavity	30
Major subcutaneous soft tissue maceration or erosion	30
Major laceration on foot pads or tongue	30
Severe joint hemorrhage	30
Joint luxation below carpus or tarsus	30
Major periosteal abrasion	30
Simple rib fracture	30
Eye lacerations	30
Minor skeletal muscle degeneration	30

Table A.1.1. Continued

Simple fracture distal to the carpus or tarsus	50
Compression fracture	50
Comminuted rib fracture	50
Amputation of 2 digits	50
Major skeletal muscle degeneration	55
Limb ischemia	55
Amputation of three or more digits	100
Any fracture or joint luxation on limb proximal to the carpus or tarsus	100
Any amputation above digits	100
Spinal cord injury	100
Severe internal organ damage (internal bleeding)	100
Compound or comminuted fracture at or below carpus or tarsus	100
Severance of major tendon or ligament	100
Compound rib fracture	100
Ocular injury resulting in blindness	100
Myocardial degeneration	100
Death	100

Table A.1.2. Comparisons of the functioning of Hancock and leg-hold traps for live capturing river otters in the Herring Bay study area, Prince William Sound, Alaska, during spring 1996. Eleven otters were captured in each type of trap.

	Type of Trap				
Trap Function	n[a]	Hancock	n[a]	Leg-hold	P-value[b]
Efficiency (captures/trap night)	292	0.038	231[c]	0.048	0.73
Escape Rate (escapes/ escapes + captures)	15	0.267	13	0.154	0.79
Malfunction Rate (traps sprung/trap night)	292	0.048	231[c]	0.065	0.52
Utility (No. latrines with traps/total no. latrines)	31	0.807	31	1.000	0.03

[a]Sample sizes are denominators in rate calculations.

[b]P-values from chi-square test on discrete data.

[c]Adjusted trap nights (i.e., corrected for malfunction of trap transmitter).

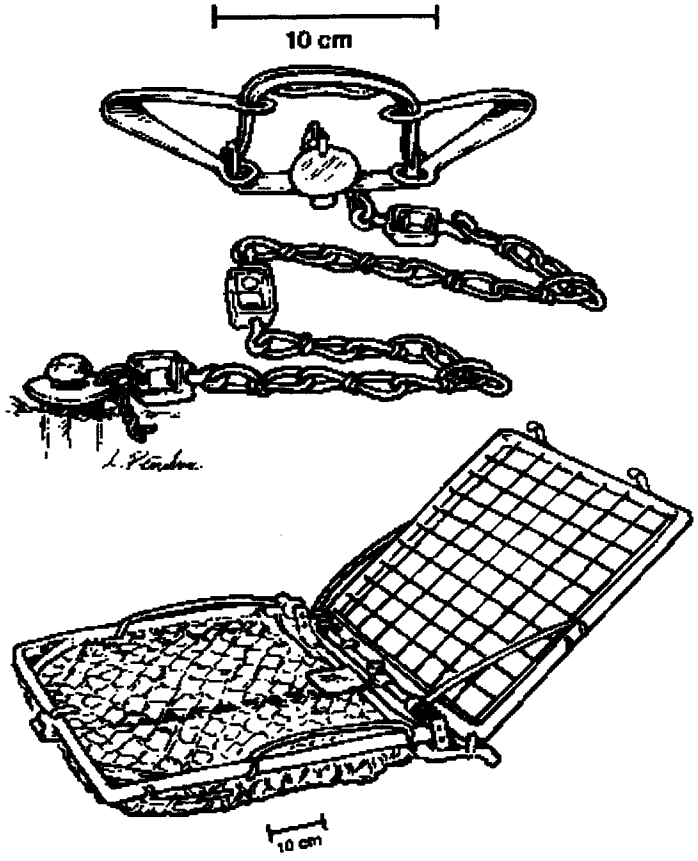

Figure A1.1 - The Sleepy Creek® #11 leg-hold trap (above) and the Hancock trap (below) we used to capture river otters. Note the large size of the Hancock trap and the swivels associated with the leg-hold trap.

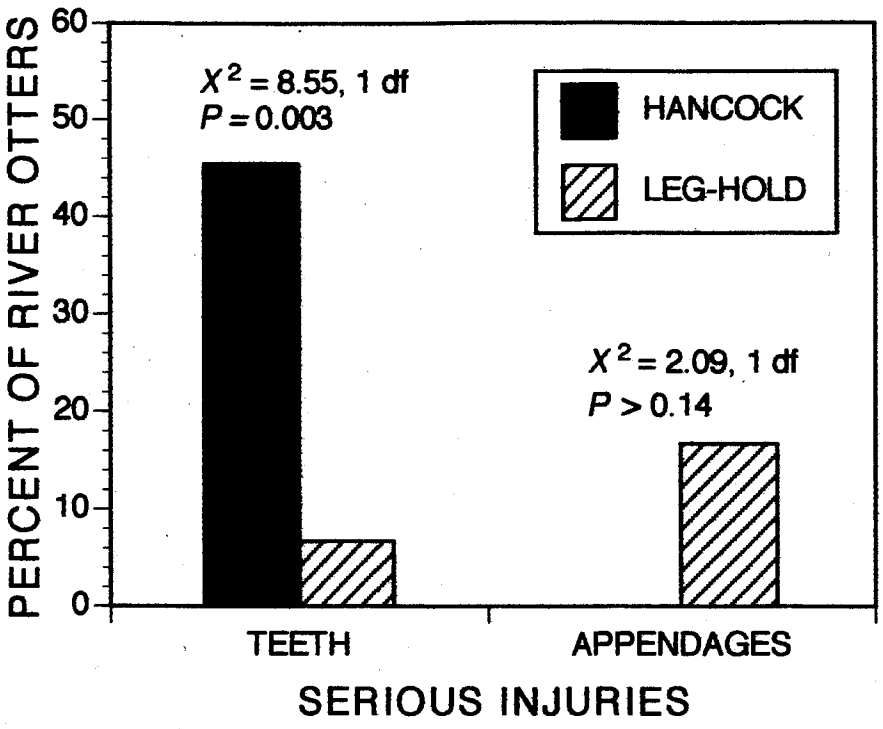

Figure A.1.2 - A comparison of serious injuries to appendages and teeth (25-100 on the trauma scale; Table A.1.1) to river otters caused by Hancock and leg-hold traps, Prince William Sound, Alaska, spring-summer 1996. Eleven otters were captured in Hancock traps, and 30 otters were captured in leg-hold traps.

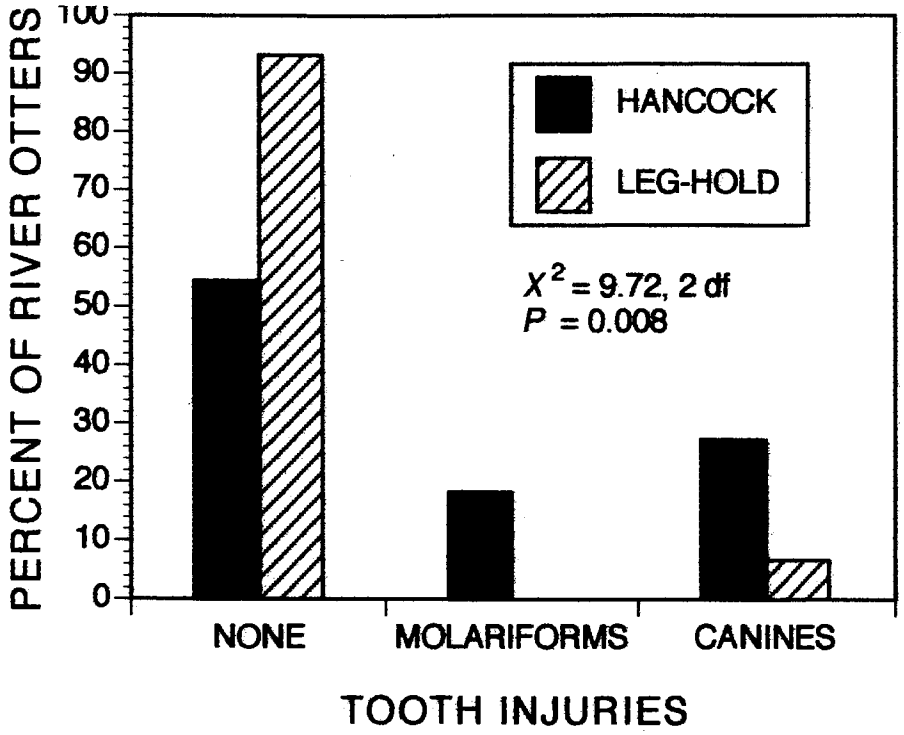

Figure A.1.3 - A comparison of the types of teeth injured by river otters in Hancock and leg-hold traps, Prince William Sound, Alaska, spring-summer 1996. Eleven otters were captured in Hancock traps, and 30 otters were captured in leg-hold traps.

APPENDIX 2

Effects of Food Resources on Spacing Behavior of River Otters: Does Forage Abundance Control Home-Range Size?[1]

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ABSTRACT

We use three analytical techniques to examine home-range dynamics of river otters in Prince William Sound, Alaska, USA, from February 1997 to January 1998 and discuss problems with analysis of linear home ranges. River otters inhabiting marine environments where fish were abundant had smaller home ranges than animals living in freshwater systems with fewer prey, whereas otters using multiple salmon runs had larger home ranges than otters in other habitats.

INTRODUCTION

River otters (*Lutra canadensis*) in Prince William Sound, Alaska, USA, occur at densities of 28-80 animals/100 km of shoreline (Testa et al. 1994), with home ranges that encompass about 20-40 km of shoreline (Bowyer et al. 1995). These otters forage intensively in intertidal and subtidal zones where they prey principally on marine fishes (Larsen, 1984; Bowyer et al. 1994, Ben-David et al., 1996, 1998). River otters living in this marine environment form large social groups ($\leq$ 18 individuals; Testa et al. 1994; Rock et al., 1994), but little is known about their spatial relationships or social structure. We tested the hypothesis that home-range dynamics and other spatial relationships of otters would be related to availability and distribution of their primary prey (fishes). We present telemetry analyses using three techniques for calculating home-range area because no single method is suitable for all purposes -- the technique most appropriate to use depends upon the hypotheses being tested (Harris et al., 1990) and data collected. Estimates of kernel density define a utilization distribution by assessing the probability that an animal will occur at particular points in space. Kernel estimators are nonparametric and can estimate densities of any shape (Seaman and Powell, 1996) by supplying a third dimension representing the amount of time an animal spent in any given area (Seaman et al., 1999); thus these methods are useful for examining the internal structure within home ranges, particularly core areas of use that may be important for foraging or den sites. Kernel estimates, however, are sensitive to autocorrelation (Harris et al., 1990), changes in smoothing parameters (Worton, 1995), and may result in over estimation of the area used (Seaman and Powell, 1996). Furthermore, kernel estimates were

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[1] Blundell, G. M., R. T. Bowyer, M. Ben-David, T. A. Dean, and S. C. Jewett. 2000. Effects of food resources on spacing behavior of river otters: does forage abundance control home-range size? Pages 325-333 in J. H. Eiler, D. J. Alcorn, and M. R. Neuman (editors). Biotelemetry 15: Proceeding of the 15th International Symposium on Biotelemetry. Juneau, Alaska USA. International Society on Biotelemetry. Wageningen, The Netherlands.

developed for analysis of spatial data occurring in two dimensions and are problematic for analysis of animals with primarily unidimensional patterns of movement such as river otters, which use a narrow aquatic-terrestrial ecotone (Sauer et al., 1999). Minimum Convex Polygons (MCP) do not have underlying assumptions of distribution, are not affected by autocorrelation (Harris et al., 1990), and are the oldest and most common method for estimating home ranges (White and Garrott, 1990; Seaman et al., 1999). The MCP technique uses the outer points in the spatial distribution to define the boundaries of the home range and may contain large areas that are never used, especially for animals that move in unidimensional space. For purposes of comparison with other studies of river otters (Reid, 1994; Green et al., 1984), we present area calculations for MCP, and area calculations for Adaptive Kernel (ADK) estimates. We also use Geographical Information System, GIS (ARC/INFO, Redlands, California) to calculate kilometers of shoreline within each of these area estimates using a method described by Sauer et al. (1999).

METHODS

Capture

We live-captured river otters using both Hancock and leg-hold traps (Blundell et al., 1999) in spring and early summer 1996-1997. Traps were placed in blind sets (i.e., no bait or lure) on trails at latrine sites and monitored by means of trap transmitters (Telonics®, Mesa, Arizona, USA) that signaled when a trap had been sprung. River otters were anesthetized with Telazol® (9mg/kg; A. H. Robins, Richmond, Virginia, USA) administered by hand injection for otters captured in Hancock traps and with Telinject® darts and a blowgun for otters captured in leg-hold traps.

Telemetry Transmitters and Radio-tracking

We surgically implanted river otters with telemetry transmitters (IMP/400/L, Telonics®, Mesa, Arizona) inserted into the peritoneal cavity through an incision made on the right side, posterior to the last rib. Each muscle layer was closed separately with simple- interrupted sutures and the skin was closed with a continuous subcuticular suture line. As a final precaution, the skin incision was sealed with surgical glue. We implanted 17 otters (12 males, 5 females) in 1996 in the Jackpot Bay area and eight river otters (5 males, 3 females) in 1997 in this area. Twelve otters (8 males, 4 females) were implanted with radio-transmitters in Herring Bay in 1997. All radio-tracking in 1996 was conducted from a boat resulting in only partial home-range information for otters using freshwater systems. For this reason, we report only data collected using aerial tracking. Otters were radio-tracked from a small fixed-wing aircraft from February 1997 to January 1998 (n = 29 occasions). Once a telemetered otter was located, Geographic Positioning System (GPS) coordinates were recorded by flying the plane directly over the location and recording latitude and longitude. Additionally, point locations for each otter were plotted on USGS maps (1:63360 scale) to provide a secondary source of location information in the event of an error in recording GPS locations. When otters were observed engaging in foraging activity, their location, distance from shore, and group size was recorded. All methods used in this research were approved by an Institutional Animal Care and Use Committee at the University of Alaska Fairbanks.

Prey Availability

We conducted scuba-diving transects in July of 1996 and 1997 in both study areas to assess fish abundance at otter latrine sites (n = 15/year) and at random sites (n = 15/year). Fish were counted

along two 30 m-transects/site and categorized into eight family groups and three size classes (< 8 cm, 8-15 cm, > 15 cm). We also assessed six random and six latrine sites in the freshwater system.

Analysis

We used CALHOME (Kie et al., 1996) to estimate home ranges (Adaptive Kernel and Minimum Convex Polygons) and Geographical Information System, GIS (ARC/INFO, Redlands, California) to calculate shoreline within these polygons (Sauer et al., 1999). We arbitrarily selected 50% Adaptive Kernel contours to examine core areas of use.

RESULTS

We obtained sufficient locations (n = 657 locations; $\bar{x}$ = 25 locations per otter) to assess home-range size for 29 river otters (20 males, 9 females) from February 1997 to January 1998. River otters inhabiting our study areas used three general habitat-prey associations: marine, freshwater, and areas with salmon runs. Prey abundance in the marine system did not differ between study areas, so we combined data from both areas to test for differences in sizes of home range between otters using different habitat-prey associations, and differences in home-range size between genders.

River otters inhabiting marine environments, where fish were abundant, had smaller home ranges than animals living in freshwater systems with fewer prey, whereas otters using multiple runs of salmon, which were geographically dispersed, had larger home ranges than otters in either marine or freshwater habitats (Table A.2.1). Shoreline within the freshwater habitat is underrepresented because locations in secondary and tertiary tributaries did not result in creek shoreline being measured near these locations.

Table A.2.1. Differences in home ranges for river otters inhabiting different habitats in Prince William Sound, Alaska, USA, (February 1997 – January 1998), pooling data from both sexes and both study areas (P-values from one-way ANOVA).

	HOME-RANGE ESTIMATES									
	MARINE			FRESHWATER			SALMON RUNS			
HOME RANGE ANALYSIS	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	P-value
Adaptive Kernel (ADK) 50% Ha	21	571	764	4	666	284	4	3648	566	0.000
Adaptive Kernel (ADK) 95% Ha	21	4255	5994	4	5327	4547	4	21185	2508	0.000
Minimum Convex Polygon 95% Ha	21	3083	6548	4	3400	3080	4	9227	1728	0.175
Km Shoreline within 50% ADK	21	7	6	4	4	3	4	15	17.8	0.018
Km Shoreline within 95% ADK	21	40	49	4	25	10	4	97	12	0.046

Males had significantly larger home ranges for both 95% estimates and core areas (50%) than did females in both marine and freshwater environments (Table A.2.2), but the proportion of the 95% area contained within the core area tended to be greater for females than for males (Table A.2.3).

Table A.2.2. Difference in size of home ranges for female and male otters in Prince William Sound, Alaska, USA, (February 1997 – January 1998), pooling data from all habitats and both study areas (*P*-values from one-way ANOVA).

	HOME-RANGE ESTIMATES						
	FEMALES			MALES			
HOME-RANGE ANALYSIS	n	$\bar{x}$	SD	n	$\bar{x}$	SD	*P*-value
Adaptive Kernel (ADK) 50% Ha	9	232	200	20	1357	1396	0.024
Adaptive Kernel (ADK) 95% Ha	9	1207	637	20	9227	8490	0.009
Minimum Convex Polygon 95% Ha	9	674	389	20	5459	6805	0.046
Km Shoreline within 50% ADK	9	4	4	20	10	6	0.016
Km Shoreline within 95% ADK	9	15	7	20	60	51	0.015

Table A.2.3. Proportion ($\bar{x}$ 50% ADK/$\bar{x}$ 95% ADK) of the shoreline distance in the entire home range (95% Adaptive Kernel; ADK) represented in the core area of use (50% ADK) for otters in our study areas in Prince William Sound, Alaska, USA, (February 1997 – January 1998).

	MARINE		FRESHWATER
SEX	Herring Bay	Jackpot Bay	Jackpot Bay
Females	20.6%	39.9%	24.3%
Males	12.8%	24.1%	17.7%

River otters in Prince William Sound exhibited intersexual overlap of home ranges but intrasexual patterns differed between the genders. Female otters had low spatial overlap and most appeared to have exclusive core areas of use, whereas male otters showed a substantial overlap in home-range areas including overlap of male-group home ranges with those of other male groups and with solitary males (50% Adaptive Kernel; Figure A.2.1).

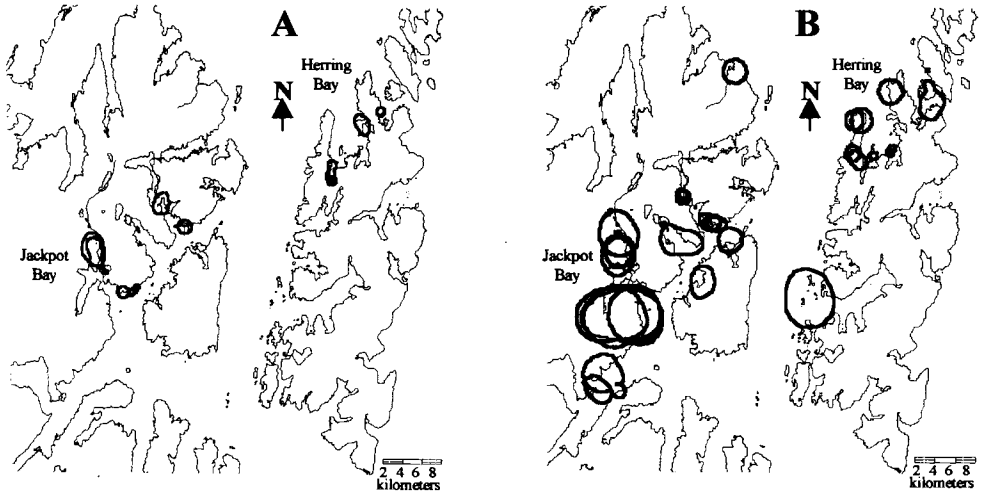

Figure A.2.1. Core areas of use (50% Adaptive Kernel) for female (A) and male (B) river otters in Prince William Sound, Alaska, USA (February 1997 - January 1998). In most instances core areas for females did not overlap. Males (both solitary and males in groups) had substantial overlap in core areas.

Each method of home-range analysis showed similar trends although MCP estimates were more conservative in both area and shoreline estimates (Tables A.2.1 and A.2.2) than ADK estimates. Standard methodologies for calculating home-range areas may not be appropriate for use in river otters because otters use narrow strips of habitat associated with the aquatic-terrestrial ecotone (Figure A.2.2).

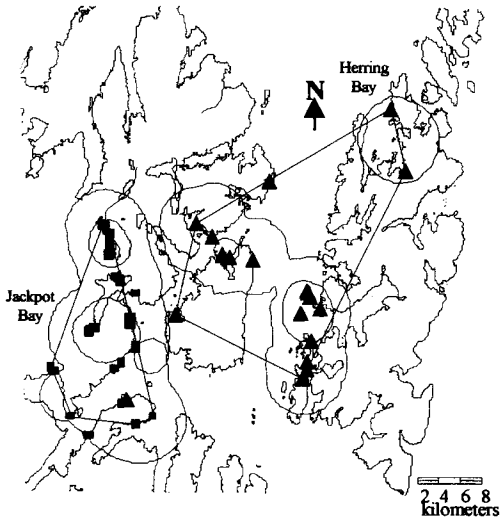

Figure A.2.2. Adaptive Kernel contours (95% and 50%) and Minimum Convex Polygons (95%) for two otters in Prince William Sound, Alaska, USA (February 1997 - January 1998), showing different patterns of movement. Symbols are the telemetry locations for each otter.

DISCUSSION

We suggest that the social structure of river otters (males primarily in groups, females mostly solitary) is resource related and has a strong influence on spatial relationships, home-range size, and diet. Spatial organization in solitary Carnivora is believed to be resource related (Sandell, 1989), with distribution of females determined by food availability, and male distribution, at least during mating season, dependent upon female dispersion. Female river otters tended to have larger core areas relative to total home-range area (Table A.2.3), suggesting that a larger proportion of their home ranges may be important for foraging. Our sample size for females, however, is small and we may not have a complete representation of space use for this gender.

The sexual dimorphism in our system is not pronounced. Males range from 10-13% larger than females in length:weight ratios, yet their home ranges in all habitats ranged from two to ten times larger than those of females (Table A.2.2). We suggest that larger home ranges for males is more likely related to females as a resource, because males use areas much larger than would be needed to support their metabolic needs (McNab, 1963; Sandell, 1989). Moreover, a smaller proportion of their total area is contained in the core for males compared with females, the area presumably of greatest importance to individuals. Additionally, we suggest that male otters traveling in groups may be foraging cooperatively. Indeed, the otters using numerous salmon runs were a group of males that traveled together once the salmon started to spawn. These males traveled greater

distances than males using other resources, but salmon runs provided rich sources of prey, likely compensating for the distance traveled.

Seaman and Powell (1996) concluded that Adaptive Kernel estimates resulted in overestimation of area and this may be occurring in our results here (Figure A.2.2). Nonetheless, the comparison of relative size of home ranges between genders and different habitat-prey associations that we present herein still provide valid assessments, and information on spatial relationships is largely independent of analysis technique.

We hypothesize that the distribution of prey, rather than simply abundance of forage, has a substantial effect on spacing behavior of otters. We will further explore this and similar hypotheses by testing for seasonal shifts in home ranges using additional radio-telemetry locations and we will investigate seasonal variation in abundance of marine fish at otter latrines and random locations. We also will use microsatellite DNA to examine the effect of genetic-relatedness on spatial relationships of river otters, and perhaps gain some insight into which males (social or solitary) gain reproductive opportunities.

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APPENDIX 3

Running head: Linear Home Ranges

LINEAR HOME RANGES: EFFECTS OF SMOOTHING, SAMPLE SIZE, AND AUTOCORRELATION ON KERNEL ESTIMATES[1]

Abstract. Simulations are necessary to assess the performance of home-range estimators because the true distribution of empirical data is unknown, but we must question whether that performance applies to empirical data. Some studies have used empirically based simulations, randomly selecting subsets of data to evaluate estimator performance, but animals do not move randomly within a home range. We created an empirically based simulation using a behavioral model, generated a probability distribution from those data, and randomly selected locations from that distribution in a chronological sequence as the simulated individual moved through its home range. Thus, we examined the influence of temporal patterns of space use, and determined the effects of smoothing, number of locations, and autocorrelation on kernel estimates. Additionally, home-range estimators were designed to evaluate species that use space with few restrictions, traveling most anywhere on the landscape. Many species, however, confine their movements to a geographical feature that conforms to a relatively linear pattern. Consequently, conventional analysis techniques may overestimate home ranges. We used simulations based upon coastal river otters (*Lontra canadensis*), a species that primarily uses the aquatic-terrestrial interface, to evaluate the efficacy of fixed and adaptive kernel estimates

[1] **Blundell, G. M., J. A. K. Maier, and E. M. Debevec. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecological Monographs 71:in press.**

with various smoothing parameters. Measures of shoreline length within contours from fixed kernel analyses and the reference smoothing parameter were best for estimates of 95% home ranges because smoothing with least squares cross validation (LSCV) often resulted in inconsistent results, excessive fragmentation, and marked underestimates of linear home ranges. Core areas (50% density contours) were best defined with fixed kernel LSCV estimates. Fewer locations underestimated linear home ranges, and there was a subtle positive relation between home-range size and autocorrelation. Generally, as location numbers increased, autocorrelation increased, but differences from the "true" home range decreased. Results were similar for our simulations and empirical data from 13 river otters. Examination of empirical data revealed that data with high positive autocorrelation illustrated seasonal reproductive activities. Because autocorrelation does not negatively influence estimates of linear home ranges, assessment of independence between data points may be more appropriately viewed as a means to identify important behavioral information rather than as a hindrance.

Key words: adaptive kernel; aquatic-terrestrial interface; autocorrelation; bandwidth; home range; fixed kernel; least squares cross validation; linear utilization distribution; Lontra canadensis*; river otter; smoothing parameters*

INTRODUCTION

Obtaining an accurate understanding of an animal's use of space based upon telemetry locations is confounded by two problems. First, the locations obtained per individual in most telemetry studies are infrequent and represent only a subsample of the true use of space (Swihart and Slade 1986, Seaman and Powell 1996), or a statistical

population of locations (Harris et al. 1990) with which we attempt to estimate a home range. Second, various home-range estimators have different statistical properties, thus, a particular analytical technique will not be appropriate for use with all distributions of data (Swihart and Slade 1986, Boulanger and White 1990, Worton 1995), and a single methodology may not be appropriate to answer all research questions (Harris et al. 1990, Worton 1995, Powell et al. 1997, Powell 2000). Comparisons of the performance of estimators on empirical data is not informative because the true home range is unknown, thus the ability of an estimator to describe the true distribution cannot be adequately assessed. Consequently, simulations of known distributions must be used to assess the performance of home-range estimators (Worton 1995). Simulations of statistical distributions, however, may not adequately reflect actual patterns of movements for animals (Boulanger and White 1990; Seaman and Powell, 1996) and thus may not be sufficient to evaluate the appropriate home-range estimator to use for a particular species or pattern of space use. Moreover, in previous simulations to assess the effects of various estimators, smoothing parameters, or number of locations (Boulanger and White 1990; Worton 1995, Seaman and Powell, 1996) on home-range estimates, data were randomly selected from simulations with no temporal consideration. Animals, however, generally do not move randomly through their home ranges (Swihart and Slade 1985*a*, Legendre 1993, de Solla et al. 1999, Powell 2000).

In this study, we used a combination of empirical data and a behavioral model to create a simulated data set from which we generated a probability distribution. Our simulations emulated sequential short-term movements within a hypothetical home range

from which we randomly selected subsets of locations in a chronological sequence at a larger temporal scale, representative of how telemetry data are collected in field studies. We used that methodology to evaluate estimates of home range.

A home range was first defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943:351). "Normal activities", which may be better expressed as the area thought to be available to the animal, cannot be objectively evaluated. Therefore a statistical definition of a home range is generally used in which a home range is defined by a utilization distribution (UD) that describes the locations of an animal over time with a relative frequency distribution (Worton 1987, 1989). To exclude excursive activity and thereby to statistically identify areas of greater use with a level of probability, estimates of home ranges are often delineated to include the animal's locations 95% of the time (White and Garrott 1990). We used animal ecology to bridge the gap between the conceptual and statistical definitions of a home range: our simulations, modeled upon a likely scenario of "normal activities" derived from empirical data and a behavioral model, were sampled to arrive at statistically defined estimates of home ranges. We assessed how well statistically defined estimates provided by kernel analyses described "normal" patterns of movements.

Kernel estimators (fixed or adaptive) determine the UD for an animal by assessing the probability of occurrence at each point in space (Worton 1987, 1989, Harris et al. 1990). Kernel methods do not require making any assumptions about the underlying distribution of the data (Worton 1987, 1989). Kernel estimators have been offered as a more accurate means of estimating home-range size (Worton 1987, 1989, 1995, Kie et al.

1996, Seaman and Powell 1996, Powell et al. 1997, Swihart and Slade 1997, Seaman et al. 1999) compared to earlier methods such as harmonic mean (Worton 1987, Boulanger and White 1990, White and Garrott 1990), ellipse (Boulanger and White 1990), minimum convex polygon (Bekoff and Mech 1984, Worton 1987), and grid cell methods (Siniff and Tester 1965, Worton 1987, White and Garrott 1990).

Methods of home-range analysis were designed primarily for species that move freely throughout the landscape (e.g., terrestrial mammals and avian species). Accordingly, in previous studies, simulated data were composed of independent "locations" that occurred anywhere in the simulated area (e.g., Seaman and Powell 1996, Seaman et al. 1999). Many species, however, confine movements to comparatively linear pathways (i.e., locations occur in a long, relatively narrow band) associated with a geographical feature on the landscape. Species such as river otters (*Lontra canadensis*; Bowyer et al. 1995, Saeur et al. 1999), beavers (*Castor canadensis*; Wheatley 1997), shorebirds (e.g., Western Sandpipers {*Calidris mauri*}; Warnock and Tekekawa 1995), mink (*Mustela vison;* Stevens et al. 1997), and turtles (e.g., *Kinosternon leucostomum*; Morales-Verdeja and Vogt 1997) use the aquatic-terrestrial interface, generally confining movements to shorelines or drainages. Reindeer (*Rangifer tarandus tarandus*; L. Nelleman 1996) tend to use ridgelines and avoid valleys in winter resulting in selective use of habitat in linear patterns. Caribou (*Rangifer tarandus*), which use migratory pathways, also conform to linear patterns of movement for at least a portion of their life histories (Maier et al. 1998). The use of standard methodologies to estimate home ranges for those linear movements may result in the inclusion of large expanses of unused area, producing

considerable overestimates of home-range size.

In this study, we determined the best (i.e., least biased and most precise) kernel method for home-range analysis for species that approximate a linear pattern of movement. We used coastal river otters as our model and based our simulated data upon actual patterns of otter movements along a coastline. We compared the performance of kernel estimates and smoothing parameters on simulations as well as on empirical data for 13 coastal river otters. Relatively few studies have used both simulations and empirical data to assess kernel estimators (Worton 1995, Seaman and Powell 1996, de Solla et al. 1999), and none have done so for linear patterns of movement.

The need for a study of this nature first became apparent during preliminary analyses of spatial data for an extensive ecological study of river otters inhabiting marine environments of Prince William Sound, Alaska (Ben-David et al. 1998, Blundell et al. *in press a*, Blundell et al. *in press b*). Several authors (Seaman and Powell 1996, Powell et al. 1997, Seaman et al 1998, Seaman et al. 1999, Powell 2000) suggested using fixed kernel estimators with least squares cross validation (LSCV) to select the bandwidth. Seaman and Powell (1996) determined that adaptive kernel estimates resulted in overestimation of home-range size and that LSCV smoothing provided the most accurate estimates. For data from many of our otters, however, the use of LSCV smoothing to estimate 95% home ranges resulted in the delineation of numerous small, disjunct contours (Fig. A3.1a). Jones et al. (1996:404-405) cautioned that LSCV smoothing produced "spurious bumps" and was "too variable (especially in the direction of undersmoothing) and hence unreliable." The fragmentation of home ranges that we observed with LSCV

smoothing may, therefore, not accurately represent true space use for coastal river otters and may exclude many important feeding areas.

River otters inhabiting marine environments forage in the intertidal and subtidal zones for marine fish and invertebrates (Larsen 1984, Woolington 1984, Stenson et al. 1984, Bowyer et al. 1994, Ben-David et al. 1998). Otters generally travel close to shore (Fig. A3.1b), usually foraging in the shallow depths as they travel (Woolington 1984, Kruuk 1995). Submerged swimming decreases energetic costs compared with surface swimming, because waves produced by an otter on the surface increases drag for the animal (Fish 1982, Williams 1989). During submerged swimming, traveling otters can forage opportunistically upon a variety of prey species encountered throughout the nearshore system (Dean et al. 2000). Thus it is reasonable to assume that, in their "normal activities" (Burt 1943), coastal river otters may use most stretches of shoreline between the disjunct contours often defined by LSCV smoothing. Smoothing that may result in "spurious bumps" (Jones et al. 1996:404) or disjunct contours, therefore, not be suitable for estimates of linear home ranges for otters. Sauer et al. (1999) circumvented fragmentation with adaptive kernel estimates and LSCV smoothing for otter data by including the shoreline between disjunct contours in estimates of linear home ranges. Their methods require considerable manual manipulation, however, and may not be practical for studies with a large number of animals.

In a previous study, kernel estimates with LSCV smoothing underestimated home ranges for empirical data for two species (de Solla et al. 1999), thus bandwidths were selected by a comparison of home-range estimates with a calculation of minimum home-

range size based on grid cells. In contrast, Worton (1995) noted that both LSCV and the reference (h_{ref}; Worton 1989) smoothing parameter (Fig. A3.1c) resulted in overestimates of home ranges, and determined that 0.8% of LSCV was the correct bandwidth for simulations based on a brush rabbit (*Sylvilagus bachmani*). Worton (1995) concluded that the choice between adaptive and fixed kernel methods for estimating size of home ranges was not as important as selection of the correct bandwidth.

Those conclusions were based upon analyses for species that moved throughout the landscape. Clearly, simulations would be required to determine which smoothing parameter is most appropriate for species that have linear patterns of movement. Therefore, we evaluated the effects of smoothing on kernel estimates of linear home ranges (i.e., 95% UD), and for intensive areas of use (i.e., core areas, 50% UD), because an estimation technique for one aspect of home-range analysis might not be good for another (Worton 1995). Indeed, Seaman et al. (1999) noted that while adaptive kernel estimates with LSCV smoothing overestimated 95% home ranges, that method provided satisfactory estimates for interior contours up to 80% of the probability distribution. Hansteen et al. (1999) used fixed kernel estimates to determine size of the home range and adaptive kernels to determine shape.

Although Seaman et al. (1999) promoted LSCV smoothing, they recognized that the use of LSCV to select bandwidths resulted in poor estimates for small sample sizes ($n < 50$ locations). Many wildlife studies, however, are limited by logistical or financial constraints to obtaining a limited number of observations per study animal. For many studies, asymptotes of area were approached with as few as 20 or 30 locations with kernel

estimates (Harris 1990, Kenward and Hodder 1996, Powell et al. 1997). Thus it is important to ascertain which kernel methods and smoothing parameters are most effective for evaluating linear home ranges with fewer data points per individual.

Additionally, some studies found that small numbers of locations overestimated home-range size (Worton 1995, Seaman and Powell 1996, de Solla et al. 1999 for simulations, Seaman et al. 1999), whereas de Solla et al. (1999, for subsamples from empirical data), and Hansteen et al. (1999) noted underestimates of home ranges with fewer locations. Seaman et al. (1999) suggested that directional differences in bias might be attributable to how home-range estimates were defined: with a utilization distribution determined by a percentage of the observations (i.e., observation density – OD), or the volume of the utilization distribution (UD). To investigate that possibility, we compared estimates obtained with both methods for small numbers of locations.

The same phenomenon that may result in selection of small bandwidths and fragmentation with LSCV smoothing (Fig. A3.1a) – multiple observations near the same location (Fig. A3.1b) – may also reflect autocorrelated data (Hansteen et al. 1997, de Solla et al. 1999). Considerable controversy has arisen regarding the importance of autocorrelation in analyses of radiotelemetry data. Swihart and Slade (1985*a*, 1986) advocated the use of Schoener's ratio (Schoener 1981) to test for independence among locations for radiotelemetry studies, and reported underestimates of home-range size with positive autocorrelation (Swihart and Slade 1985*b*). Reynolds and Laundré (1990) reported that independent data resulted in underestimates, but Anderson and Rongstad (1989) reported similar estimates of home ranges with random and systematic sampling,

even though systematic sampling tended to be autocorrelated. No relationship was found by de Solla et al. (1999) between home-range size and autocorrelation for field data, and the authors suggested that the underestimates reported by Swihart and Slade (1985*a*) were likely a result of a shorter total sampling period which provided less information about space use. Swihart and Slade (1997) conducted further simulations with kernel estimates and noted less sensitivity to autocorrelation than with other home-range estimators, concluding that moderately autocorrelated data were acceptable with kernel analyses.

Generally, kernel analyses are less sensitive to autocorrelation than are other home-range estimators (Swihart and Slade 1997, de Solla et al. 1999); at least for species that exhibit unrestricted patterns of movement. We examined the effects of autocorrelation on kernel estimates of linear home ranges. Thus the objectives for this study were as follows: 1) to determine the most accurate method of estimating linear home ranges (95% and 50% core areas); 2) to simultaneously assess the effects of kernel method and smoothing parameter, number of locations, and autocorrelation on estimates of linear home ranges; and 3) for small numbers of locations, to compare 95% home ranges between estimates based upon a percentage of the observations (OD), and the volume of the utilization distribution (UD). To accomplish these objectives we used empirical data and a behavioral model as the basis for simulations, and a temporal sampling scheme representative of how telemetry data are collected in the field.

METHODS

Simulated data

We selected one river otter from among 55 otters for which we had telemetry data to use as an empirical base for our simulations. The otter (JP11, Fig. A3.2) appeared to exhibit movements typical for otters inhabiting marine environments in western Prince William Sound, Alaska (Testa et al. 1994, Rock et al. 1994, Bowyer et al. 1995, Sauer et al. 1999). In 1996 (Fig. A3.2a), 26 locations were obtained for JP11 an average of 56.7 hours apart (SE = 6.0, range = 12 - 170h) and subsequent locations were an average of 1639 meters apart (SE = 211, range = 0 – 3790m). In 1997 (Fig. A3.2b), 31 locations were obtained an average of 13.1 days apart (SE = 4.2, range = 3 – 83d) and subsequent locations were an average of 1900 meters apart (SE = 304, range 53 – 5490m). In 1998 (Fig. A3.2c), 36 locations were obtained ($\bar{x}$ = 9.9d apart, SE = 0.75, range = 3 – 21d) and subsequent locations were an average of 2210m apart (SE = 327, range = 44 –6364m). The general pattern of space use for JP11 was similar among years: ≥ 71% of locations in all years occurred in the same bay, with occasional excursions to a neighboring bay (15.4% and 3.2% of locations in 1996 and 1998, respectively) and a freshwater lake (22% and 25.8% in 1997 and 1998, respectively). The mean distance between locations also was similar among years. Spatial similarities were apparent regardless of whether data were collected during an intensive monitoring period of 2 months (Fig 2a, random start times throughout the 24-h day during summer; locations in freshwater lake not obtainable from marine-based boat), or collected throughout the year from a fixed-wing aircraft (Fig. A3.2b and c). Therefore, we used all locations for JP11 to define the extent of the hypothetical home range for our simulations and to identify locations within that range that would see greater use by the simulated otter.

We used data from behavioral observations obtained in previous studies of coastal river otters in western Prince William Sound, Alaska, (Testa et al. 1994, Rock et al. 1994, Bowyer et al. 1995, Sauer et al. 1999) to evaluate short-term patterns of movement for otters. We analyzed data from 41 records of observations of 12 river otters, totaling 182 observation hours, often involving 24-h observation periods following the same focal otter. The length of observed resting periods ranged from 1.1 – 17.3h ($\bar{x}$ = 7.2h, SE = 1.1), and periods of activity (i.e., movement primarily on water, interrupted by visits to land ranging from 1 minute to <1h) ranged from 3 minutes to 8.4h ($\bar{x}$ = 1.7h, SE = 0.4). Average distance traveled during activity periods was approximately 2.3 km (SE = 0.3, range = 0.4 – 5.3 km) at a rate of approximately 47 meters/minute (SE = 8, range 3 – 161m). There was no significant correlation between time spent moving and distance covered (r = 0.255): the otter with the longest observed activity period (8.4h) covered ≈3.2 km, the most rapid movement (≈161meters/minute) was accomplished in 10 minutes, the longest distance traveled in one observation period (≈5.3km) occurred in 55 minutes. Otters generally traveled close to shore ($\bar{x}$ = 5.1 meters from shore, SE = 0.9, range 1 – 80m, n = 119 distances recorded,) usually foraging as they traveled, and there was no obvious temporal pattern for activity or rest periods. Otters were observed crossing small landmasses from one body of water to another (< 1 km), and swimming to an island or across the mouth of a bay (≤ 1.2 km).

River otters scent mark at communal latrine sites (Testa et al. 1994, Bowyer et al. 1995, Kruuk 1995, Ben-David et al. 1998). Accordingly, during behavioral observations, otters frequently visited latrine sites – up to 9 times during a single activity period. Similar

rates of visitation by individual otters were obtained from removal and re-sampling of feces in weekly intervals at known latrine sites (Testa et al. 1994). We used data from those behavioral observations as a model (defining rates and patterns of movement) to create a data set of known distribution, simulating otter movements every two hours within a hypothetical home range defined by data from JP11 (Fig. 2).

A coverage was generated in ARC/INFO (ESRI, Redlands, CA) that included all point locations for JP11 ($n = 93$, Fig. A3.2) as well as locations for all known latrine sites in that area ($n = 66$). In a new coverage superimposed over the empirical data, we created a reference data set of 1500 locations, manually entering "locations" representative of movements every two hours for 125 days (Fig. A3.3), following the rules of otter movements obtained from the behavioral data. The simulated otter repeatedly traversed the coastline within the home range, generally traveling close to shore, usually in the same direction along the shore during an activity period. Occasionally the simulated otter made short overland and water crossings commensurate with data from behavioral observations. The simulated otter visited latrine sites briefly (emulating scent-marking activity) and for extended resting periods as per observational data.

Fifty eight % of the locations in the reference data set corresponded to locations used by JP11 (within 50m), and 21 % were associated with latrine sites (within 100m). The low percentage of locations at latrine sites is due to a small number of latrines ($n = 22$) identified in the bay where the majority of locations occurred (Fig. A3.3). Similarly, only 21% of the actual locations for JP11 were associated with latrine sites. The mean linear distance between locations for all 1500 data points (including distances of 0 - 25m

measured during resting periods) was 423m (SE = 11.8); maximum distance traveled in 2 hours was 4.1 km (33.9 meters/minute). Resting periods averaged 5.6h (ranging from 2 to 16 hours) and generally occurred at least once in every 24-h period (i.e., 1 longer or multiple shorter resting periods/24h). Analogous with data from JP11 (Fig. A3.2), the majority of locations (82.9%) were concentrated in a single bay, with occasional excursions to two areas: a lake which was visited several times for a period of days each visit (10.5% of the locations), and a neighboring bay that was visited several times during a single day or overnight excursion (6.7% of the locations, Fig. A3.3).

A utilization distribution (UD, Fig. A3.4) was created to assign a probability of occurrence between locations in the reference data set (Fig. A3.3). This "true" UD for our simulated otter consisted of 1500 bivariate normal distributions, each centered on one of the 1500 locations in the reference data set. Locations were randomly generated from this UD (Fig. A3.4) to create simulated data sets of n = 15, 25, 50, 100, and 200 locations. One hundred replicate data sets were generated for each sample size. To maintain the chronological nature of the location data, the following two-step procedure was used:

1. For n = 15, 25, 50, and 100, we randomly selected 15, 25, 50, or 100 days from the 125 days in the reference data set, such that the selected days moved forward in temporal sequence. For each day chosen, we randomly selected a location from the 12 observations for that day. For n = 200, we randomly selected a single location from each of the 125 days plus an additional location from each of 75 randomly selected days (125 + 75 = 200). Days with multiple locations were

sampled without replacement, and temporal sequence was maintained for the 200 locations.

2. We used each location selected in step 1 as the mean of a bivariate normal distribution with a standard deviation (SD) of 100 m in each direction. One hundred meters was chosen to create a distribution congruent with otter movements along a coastline (Figs. 1 and 2). The SD needed to be a reasonable measure, with respect to linear length of the area traversed by an otter (Figs. 1 and 2), without deviating too far from shore. The mean distance from shore (5.1m) reported for the observational data used for our behavioral model may have been biased by observation method (observers in a small boat traveling close to shore). Therefore, we calculated the distance of locations from shore for 13 otters that were radiotracked with aerial telemetry ($\bar{x}$ = 68.6m, SE = 4.3, n = 408). Thus a SD of 100m for our UD represents a reasonable distribution for simulations of otter movements along a shoreline.

Empirical data

To compare simulated with empirical data, we selected a single year of data from one study area (Herring Bay, Prince William Sound, Alaska, 60° 30'N, 147° 40'W), which constituted the least variable data set among 3 years and 3 study areas. We selected only otters with ≥ 15 locations ($\bar{x}$ = 29.8 locations, SE = 1.4, range 20 – 37), because the minimum number of locations in the simulated data was 15. The 13 otters used for our comparisons (also used for our calculations of mean distance from shore) consisted of adults and juveniles of both sexes. Otters were captured using leg-hold traps (Blundell et

al. 1999) and implanted with radio-transmitters (Blundell et al. *in press*). For further details on telemetry methods see Blundell et al. (*in press*).

Home-range analysis – kernel density estimation

To obtain kernel density estimates, a kernel, essentially a "scaled down probability density function" (Worton 1989), is placed over each data point and the average densities of the kernels are estimated at each intersection of a grid, superimposed over the data (Silverman 1986, Seaman and Powell 1996). The smoothing parameter (h) controls the amount of variation in each component of the estimate, defining the bandwidth of the kernel. Narrow kernels reveal small-scale details (i.e., nearby observations exert the greatest influence on the density estimates) whereas wide kernels are influenced by distant observations and thus disclose the general shape of the distribution (Silverman 1986, Seaman and Powell 1996). Fixed kernel estimates fix the value of the smoothing parameter over the plane. Adaptive kernel estimates vary the amount of smoothing, such that areas with a low density of data points, generally at the tails of the distribution (Silverman 1986, Worton 1995), receive greater smoothing (i.e., have high values of h) and areas with high density receive less smoothing (Silverman 1986, Worton 1989). The optimum value of h, or the reference bandwidth (h_{ref}; Worton 1989, 1995), has been analytically determined for multivariate standard normal distributions (Silverman 1986). Least squares cross validation (LSCV) resembles a jackknife estimator, using subsets of data to determine the bandwidth that yields the lowest measure of estimated error (i.e., the difference between the unknown true density function and the kernel density estimate; Silverman 1986). If data are nonuniform, LSCV cannot minimize the integrated square

error (Silverman 1986) and home range estimates revert to the optimum value of h (h_{ref}).

95% kernel density estimates and smoothing parameters

Estimates of 95% home ranges were obtained for all numbers of locations with an adaptive kernel (adk) estimate and the reference smoothing parameter (h_{ref}) to select the bandwidth. Fixed kernel (fx) estimates with h_{ref}, and 0.8% of h_{ref} (as per Worton 1995) were also obtained. Adaptive and fixed kernel estimates with LSCV smoothing were obtained for all numbers of locations with the exception of $n = 1500$, which could not be calculated because of computational limitations. Grid size for all kernel estimates was 40 x 40, the default for Ranges V. For all numbers of locations, the 95% density contours were calculated for the utilization distribution, which include the selected proportion of observations or the observation density (OD). A subset ($n \leq 25$) of kernel contours were calculated based on the density or volume of observations to determine utilization distribution (UD).

Core Area

Numerous methods have been suggested for determining core areas in home ranges. In an attempt to limit the scope of this study, we wished to evaluate only one method and one interior contour that potentially represented the core area. Kenward and Hodder (1996) suggested identifying the core area by examining the UD in a plot of the relationship between percentage of locations and area used. The core area excludes most of the excursive activity, and for different animals in a population, the core area tends to be similar in size whereas excursive areas vary among individuals (Kenward and Hodder 1996). Thus if all individuals are using space in a similar manner, the percentage of fixes at

which the variance in range size among individuals reaches a minimum represents the core area (Kenward and Hodder 1996). We used that approach and our empirical data for 13 otters to crudely assess the core area for the kernel methods that we evaluated. The percentage of fixes that excluded most excursions varied, depending upon smoothing, thus the mean percentage of fixes was selected where that minimum variance was achieved ($\bar{x}$ = 50%, SE = 3.5). Thus 50% core areas were estimated for fixed and adaptive kernel methods with LSCV and h_{ref} smoothing. Ranges V software (Kenward and Hodder 1996) was used for all home-range analyses.

Shoreline measurements

Polygon coverages were generated for the contours resulting from each of the kernel methods with the Geographic Information System (GIS) ARC/INFO (ESRI, Redlands, California). Those coverages were overlaid onto an arc coverage depicting the shoreline in the pertinent geographic area and then were used to cut the shoreline using the clip command. This resulted in fragments of shoreline, in the form of an arc coverage, contained within each home-range contour. The shoreline coverage must be an arc coverage for the result to include only lengths of shoreline, because a polygon coverage sums the lengths of shoreline and the length of the home-range contour. Arc lengths (i.e., shore lengths) are automatically included in the arc attribute table, which accompanies each arc coverage. Shore lengths were unloaded into individual data files using the Tables module of ARC/INFO.

Home-range Size: Bias and Precision

We compared home-range estimates with "true" values from our simulated utilization

distribution to determine bias and precision. Here we define bias as the difference between the mean estimated home-range size and the true home-range size. Precision is a measure of variability or uncertainty in the estimate and is calculated by its standard error.

To determine true values, we placed a grid over the pertinent geographic area of our simulated distribution (UTM: X = 436,000 to 443,300, Y = 6,692,800 to 6,702,700) and approximated the volume under the UD surface for each grid cell. A grid resolution of 20 m was selected because it was small enough to capture the relevant characteristics of the UD, yet not so small that the effort would become computationally difficult. A point on the surface of the UD was calculated for the center of each grid cell and multiplied by 400 (20×20) to obtain a volume for each cell. We then divided each cell volume by the sum of all cell volumes to convert to probabilities, which, along with the shoreline and area of each cell, were sorted in descending order. We added the cell probabilities from largest to smallest until the cumulative sum first reached or exceeded 0.95. The corresponding cumulative sum of shoreline and area were taken as the true 95% shoreline and area, respectively.

To evaluate the performance of each kernel method and smoothing parameter and their relative sensitivity to number of locations, we compared the 95% estimates of km shoreline and area with the 95% "true" shoreline and area, respectively. We calculated the mean estimated shoreline and area for each simulation and its associated standard error:

$$\overline{w} = \frac{1}{n_s} \sum_{i=1}^{n_s} w_i$$

$$SE_{\overline{w}} = \sqrt{\frac{1}{n_s - 1}\sum_{i=1}^{n_s}(w_i - \overline{w})^2}$$

where w_i is the estimated shoreline or area for the i^{th} replicate and n_s is the number of replicates in the simulation. We also calculated the root mean squared error (RMSE) to evaluate the effect of kernel method on the bias and precision of the estimates:

$$RMSE = \sqrt{b^2 + SE_{\overline{w}}^2}$$

where b is the bias defined as $\overline{w} - \omega$, with ω being the "true" shoreline or area.

Autocorrelation

We tested for independence of locations in our simulated and empirical data by calculating Schoener's ratio (Schoener 1981, Swihart and Slade 1997), defined as t^2/r^2, where t^2 is the mean squared distance between successive observations:

$$t^2 = \frac{1}{m}\sum_{i=1}^{n-1}(x_{i+1} - x_i)^2 + \frac{1}{m}\sum_{i=1}^{n-1}(y_{i+1} - y_i)^2$$

m denotes the number of pairs of successive observations ($m = n - 1$ if all pairs are used) and i describes the order in which the observations were collected. The mean squared distance from the center of activity, or r^2, is calculated as follows:

$$r^2 = \frac{1}{n-1}\sum_{i=1}^{n}(x_i - \overline{x})^2 + \frac{1}{n-1}\sum_{i=1}^{n}(y_i - \overline{y})^2$$

We calculated t^2/r^2 for the 100 replicates of each sample size in our simulated data and for each otter in our empirical data.

Statistical analyses

Two-tailed Pearson correlation was used to assess the relationship between estimates of km shoreline and area, and the relationship between autocorrelation and estimates of linear home ranges. If positive autocorrelation (reflected by values of $t^2/r^2 < 2$) resulted in underestimates of home-range size as suggested by Swihart and Slade (1985*b*), we would expect to see a positive correlation between measures of linear home ranges and t^2/r^2.

To simultaneously evaluate the effects of numbers of locations and autocorrelation and their interaction, a multivariate analysis of variance (MANOVA) was conducted for each kernel method. The number of locations was entered as the independent variable with autocorrelation (t^2/r^2) as a covariate, and shoreline length and number of contours were entered as dependent variables. The correlation between shoreline estimates and number of contours also was determined. Post-hoc multiple comparisons (Scheffe) were used to compare among numbers of locations and numbers of contours. A comparison among kernel methods was conducted with a saturated-model MANOVA to examine the effects of all possible interactions (kernel methods, number of locations, and autocorrelation) on estimates of shoreline length and number of contours. Post-hoc comparisons were made among kernel methods for estimates of shoreline length and numbers of contours.

For empirical data, where number of locations was more variable and only 13 otters were evaluated, locations and autocorrelation were both entered as covariates in a MANOVA which compared the effects of kernel methods, number of locations, and

autocorrelation on estimates of shoreline length and number of contours. Sex also was entered as a covariate to control for differences in home range size between sexes. Post-hoc comparisons were conducted among kernel methods. Statistical analyses were performed with SPSS (V 7.0 1995) or S-Plus (V 2000).

RESULTS

Simulated data

95% kernel estimates and smoothing parameters. – Estimates of kilometers shoreline (Fig. A3.5a) and area estimates (Fig. A3.5b) showed the same general trend; with the exception of fx LSCV, all methods resulted in an increase in estimates of home-range size as the number of locations increased. Linear estimates underestimated true kilometers shoreline with fewer locations, and estimates of area generally overestimated true area for most kernel methods (Fig. A3.5). Both kernel methods with LSCV smoothing generally showed greater variance for all numbers of locations than did kernel methods with h_{ref} smoothing. High variance also was noted for adk h_{ref} with <100 locations, compared with fx h_{ref} and fx 0.8 (Fig. A3.5). There was a decrease in variance and range with increasing numbers of locations (Fig. A3.5) for all kernel methods except for estimates of area with adk LSCV in which standard error (SE) remained high for all numbers of locations (Fig. A3.5b).

For linear estimates, the reference smoothing parameter (h_{ref}) resulted in the most accurate estimates: adk h_{ref} had the lowest values of RMSE, followed by fx h_{ref} (Fig. A3.6a) but variance was greater for adk h_{ref} (Fig. A3.5a). For ≥ 25 locations, differences between adk h_{ref} and fx h_{ref} estimates were small (≤ 1.7 km; Fig. A3.6a). Fixed kernel

estimates with LSCV smoothing resulted in the least accurate measures of kilometer shoreline; fx 0.8 and adk LSCV were intermediate.

For area estimates, fx LSCV and fx 0.8 had the lowest RMSE values, with greater accuracy for fx LSCV with ≥50 locations. Both adaptive kernel methods resulted in high RMSE values, but adk h_{ref} was less accurate than adk LSCV (Fig. A3.6b). Neither adaptive kernel estimate showed a consistent trend with increasing numbers of locations (Fig. A3.6b) due to a reduction in RMSE for estimates with 50 locations compared with estimates obtained for 25 and 100 locations.

Linear estimates were highly correlated with area estimates: adk LSCV $r = 0.74$, adk h_{ref} $r = 0.95$, fx LSCV $r = 0.82$, fx h_{ref} $r = 0.86$, fx 0.8 $r = 0.96$ (two-tailed Pearson correlation). Consequently, results of statistical analyses (excluding bias measurements, Fig. A3.5) would likely be similar between those two measures of home-range size. For that reason, and because home-range contours often delineate large areas not used by species that confine locations to the shoreline (Figs. 1 and 2), generally resulting in overestimates of the actual area used (Figs. 1c and 5b), further analyses were conducted only for shoreline estimates.

Linear estimates for all kernel methods were significantly affected by increasing numbers of locations (Table A3.1) with the exception of adk LSCV, which showed no trend (Table A3.1, Fig. A3.5a). Post-hoc comparisons among numbers of locations (Table A3.1) revealed that estimates of shoreline length generally were similar with 25 and 50 locations, and estimates with ≥100 locations did not differ from "true" for all methods except fx LSCV and fx 0.8 (Table A3.1, Fig. A3.5a) which underestimated true.

To determine whether the number of contours produced by each kernel method was influencing the home-range estimates, we plotted the relationship between the amount of fractionation and number of locations for each method (Fig. A3.7). LSCV smoothing resulted in more contours and considerably more variance than did h_{ref} smoothing. Variance generally was greater for contours produced by adk LSCV methods and number of contours was greater for fx LSCV methods (Fig. A3.7). There was no relationship between shoreline estimates and number of contours for fx LSCV (Table A3.1) but the relationship was significant for all other kernel methods. For adaptive kernel methods, the relationship was negative (i.e., more contours corresponded to lower estimates of linear length, Table A3.1). There was a weak positive correlation for fx h_{ref} and fx 0.8 (Table A3.1). Although fx LSCV showed no significant correlation between contours and linear home ranges (Table A3.1), as numbers of locations increased, number, range, and variance of contours also increased (Fig. A3.7), and fx LSCV estimates provided the least accurate estimates of km shoreline (Figs. 5a and 6a).

Shoreline estimates differed among kernel methods (Table A3.1), but post-hoc comparisons noted that fx h_{ref} estimates did not differ from those with adk LSCV (Table A3.1), largely due to high variance and a lack of trend in estimates with adk LSCV (Figs. 5a and 6a). There were no homogeneous subsets among kernel methods for number of contours produced (Table A3.1, Fig. A3.7). Only fx 0.8 showed a significant effect of location number on contours (Table A3.1). Estimates with the utilization distribution based upon the percentage of observations (or observation density – OD) did not differ from those based upon the volume of the utilization distribution (UD) for fx LSCV or fx

h_{ref} methods (Fig. A3.8).

Core areas. – Estimates of km shoreline contained within the 50% core area of intensive use underestimated true shoreline (Fig. A3.9a) for all techniques with $n \leq 25$ locations. LSCV smoothing resulted in underestimates for $n \leq 50$ locations, and yielded more contours with greater variance than did h_{ref} smoothing (Fig. A3.9b). With ≥100 locations, h_{ref} smoothing resulted in moderate overestimates of true shoreline in core areas (Fig. A3.9a). Shoreline estimates and number of contours were similar for adk h_{ref} and fx h_{ref} estimates (Fig. A3.9).

RMSE values were similar between smoothing parameters: h_{ref} smoothing provided a more accurate measure of core shorelines than did LSCV smoothing for both adaptive and fixed kernel methods (Fig. A3.10). Differences in RMSE values were minor for all kernel methods: ≤ 1.3km at $n = 50$ locations between the least accurate fx LSCV and the most accurate fx href estimate (Fig. A3.10).

Shoreline estimates of core areas were significantly affected by increasing numbers of locations for all kernel methods (Table A3.2, Fig. A3.9a). Homogenous subsets among number of locations occurred for fx LSCV and fx h_{ref} (Table A3.2). The number of locations did not have a significant effect on number of contours produced for any kernel method, and there was a significant correlation between number of contours and shoreline estimates for all methods (Table A3.2). With the exception of fx LSCV, the correlation was negative and was most pronounced with adk LSCV and fx h_{ref} methods (Table A3.2).

Empirical data

95% kernel estimates and smoothing parameters. – The relationship among kernel

methods generally was similar for 95% estimates of km shoreline for empirical data (Fig. A3.11) compared with similar numbers of locations for simulations (n = 25 and 50, Fig. A3.5a). LSCV smoothing resulted in the smallest estimates of km shoreline, but adk LSCV estimates were more similar to fx LSCV estimates for empirical data than for simulations. Adaptive kernel estimates with h_{ref} smoothing yielded the largest estimates of km shoreline. The number of contours resulting from each kernel method also was similar between empirical (Fig. A3.11b) and simulated data (Fig. A3.7). Fragmentation was still prevalent with fx LSCV estimates and was more pronounced with adk LSCV estimates and our empirical data (Fig. A3.11b) than with our simulations (but note the large increase in number of contours between adk LSCV n = 25 and n = 50, Fig. A3.7). There was a significant negative correlation between contour number and shoreline estimates for adk LSCV (P = 0.02, r = -0.63), and a positive correlation for fx 0.8 (P = 0.05, r = 0.56). All other correlations were not significant.

A comparison among kernel methods, controlled for sex differences, noted no differences among methods in 95% shoreline estimates (Table A3.3) or contours (P = 0.07), and no effect of number of locations (P = 0.3, and P = 0.1, respectively). Shoreline estimates differed between sexes (Table A3.3), but contour numbers were similar (P = 0.1). Post-hoc multiple comparisons (Scheffe), controlled for sex differences, noted no difference in shoreline estimates among kernel methods (Table A3.3, Fig. A3.11a). The numbers of contours did not differ between kernel methods with h_{ref} smoothing or between those with LSCV smoothing (Figure 11b).

Because RMSE was similar between adaptive and fixed kernel methods with h_{ref}

smoothing for simulated data (Fig. A3.6a), we examined the nature of the differences between the 2 methods for empirical estimates (Table A3.3) to aid in determination of the better kernel method for empirical data. Both methods resulted in similar estimates (< 1 km difference) for 6 otters, but adk h_{ref} was more variable (Fig. A3.11) and resulted in estimates up to 11.6 km greater than with fx h_{ref} estimates (Table A3.3). Commensurate with our results for simulations, LSCV smoothing yielded inconsistent results. For 46% of the otters (n = 6), LSCV smoothing could not minimize the error beyond that provided by h_{ref} smoothing, thus both smoothing parameters yielded identical estimates of shoreline for adaptive and fixed kernel methods (Table A3.3).

As with our simulations, there was no difference in our empirical data between fixed kernel estimates modeled on the density or volume of locations to obtain a utilization density (UD) or utilization distributions obtained with a percentage of fixes or observation density (OD). Results were as follows: fx h_{ref} P = 0.7, UD $\bar{x}$ = 19.9, SE = 12.8, OD $\bar{x}$ = 21.1, SE = 12.9; fx LSCV P = 0.7, UD $\bar{x}$ = 15.3, SE = 13.7, OD $\bar{x}$ = 15.2, SE = 13.

A test of 3 otters revealed that an asymptote was approached for 95% shoreline estimates with fx h_{ref} analyses at the same number of locations as for area estimates, and shoreline estimates were highly correlated with area estimates for all 13 otters (r = 0.96, Pearson correlation). Therefore, calculation of area asymptotes for fx h_{ref} estimates with Ranges V software should provide a good indication of asymptotes for km shoreline. All 13 otters approached an asymptote with an average of 19.4 locations (SE = 2.5, range 5 to 34 locations).

Core areas. – Similar results were obtained for each kernel method with both

empirical data (Fig. A3.12) and simulations (Fig. A3.9a) for shoreline estimates of 50% core areas: h_{ref} smoothing yielded the largest estimates and generally resulted in a mean of < 2 contours. In contrast to simulations, fx LSCV methods resulted in larger shoreline estimates than did adk LSCV methods (Fig. A3.12). Kernel estimates with LSCV smoothing resulted in more fractionation for 95% estimates with our empirical data (Fig. A3.12b) than for our simulations for n = 25 and 50 locations (Fig. A3.7), particularly for adk LSCV, but fx LSCV still yielded the most contours (Fig. A3.12b). Both kernel methods with h_{ref} smoothing had significant negative correlations between contour numbers and shoreline estimates (adk h_{ref} $P = 0.02$, $r = -0.64$; fx h_{ref} $P = 0.02$, $r = -0.63$, Pearson correlation).

There were no differences among kernel methods, controlled for sex differences, for estimates of shoreline within 50% core areas ($P = 1.0$, MANOVA), or number of contours ($P = 0.5$, MANOVA). Both shoreline estimates and contour numbers showed a significant effect of number of locations ($P = 0.002$ and $P = 0.04$, respectively) and shoreline estimates differed between sexes ($P = 0.001$) but contours were similar between sexes ($P = 0.1$).

Autocorrelation

Simulated data. – As number of locations for our simulated data increased, the positive autocorrelation increased (i.e., Schoener's ratio, or t^2/r^2, decreased, Table A3.4). For each kernel method assessed individually, autocorrelation did not have an effect on 95% shoreline estimates or number of contours ($P \geq 0.1$, MANOVA; Table A3.1), and the interaction of t^2/r^2 and n was significant only for adk h_{ref} shoreline estimates and fx 0.8

contours (Table A3.1). A saturated-model MANOVA comparing among all kernel methods noted significant effects of t^2/r^2 and the interaction of t^2/r^2 * *n* for shoreline estimates, but not for number of contours (Table A3.1).

Power ($\alpha = 0.05$) to detect an effect of autocorrelation (t^2/r^2) on shoreline estimates was generally low for individual methods of 95% shoreline estimates (adk LSCV = 0.2; adk $h_{ref} = 0.3$; fx LSCV = 0.09; fx $h_{ref} = 0.4$; fx 0.8 = 0.3). Power for t^2/r^2 * *n* was higher (ranging from 0.1 to 0.7). For the saturated model comparing among kernel methods, power to detect an effect of autocorrelation among shoreline estimates was 0.7; t^2/r^2 * *n* power = 0.7; t^2/r^2 * kernel method = 0.09; and t^2/r^2 * *n* * kernel method = 0.7. Generally there was no relationship (two-tailed Pearson correlation) between t^2/r^2 and estimates of km shoreline (Table A3.5). For those relationships that were significant, the correlations were negative (i.e., greater positive autocorrelation corresponded to larger shoreline estimates) but not pronounced ($r \leq -0.28$, Table A3.5).

Autocorrelation had no significant effect on estimates of shoreline length or contours for 50% core areas for individual methods, and only fx LSCV showed a significant effect of the interaction between t^2/r^2 and *n* (Table A3.2). The saturated model comparing among kernel methods showed a significant effect of autocorrelation (Table A3.2).

Empirical data. – Schoener's ratio ranged from 0.21 to 2.24 for radiotelemetry data collected for 13 otters over one year of time (Table A3.6). There was no difference in t^2/r^2 values between sexes, age class, or their interaction (Table A3.6). A saturated-model MANOVA assessing 95% shoreline estimates (Table A3.3) and number of contours

showed no effects of autocorrelation ($P = 0.9$, and $P = 0.07$, respectively). Interactions between kernel methods and autocorrelation, number of locations and autocorrelation, and a 3-way interaction also were not significant for shoreline estimates or contours ($P \geq 0.8$ and $P \geq 0.09$, respectively).

We had less power to detect effects of autocorrelation with our empirical data than with our simulated data (power ranged from 0.05 to 0.4 for empirical data). There was, however, no correlation between autocorrelation (t^2/r^2) and shoreline estimates of 95% home ranges (Table A3.3) or core (50%) home ranges for otters, regardless of kernel method. P values ranged from 0.7 to 0.9 (two-tailed Pearson correlation) even though extreme positive autocorrelation was noted in numerous cases (54% of the otters had t^2/r^2 values < 1.5 and only 23% had t^2/r^2 scores > 2; Table A3.6).

DISCUSSION

95% home-range estimates

We believe our approach to simulations provides a more realistic test of home-range estimates than did previous studies. Whereas for other simulations, data were randomly selected with no temporal consideration, our simulations were based upon a behavioral model of sequential movements, ostensibly emulating "normal activities" (Burt 1943). From that distribution, we randomly selected subsets of locations in a chronological sequence representative of how telemetry data are collected in field studies to obtain statistically defined estimates of home ranges. An animal's movement within its home range is generally not a random process (Swihart and Slade 1985*a*, Legendre 1993, de Solla et al. 1999, Powell 2000). Usually some areas are used more often than others

are; thus multiple locations clustered together are not unexpected. Our simulation and sampling method was more likely to result in clustered locations than would random sampling from a statistical distribution of independent locations, as previous simulation studies have done (e.g., Seaman and Powell 1996).

Whereas radiotelemetry studies with Global Positioning System (GPS) transmitters allow for nearly continuous collection of location data for larger animals, most aerial telemetry studies are limited in the number of locations which can be obtained. Such studies are thus relying upon only a subset of data (i.e., infrequent locations) to reveal the "true" home range. Our approach to simulations provides a more accurate assessment of how well kernel methods identify the actual patterns of movement that describe a complete home range when limited numbers of locations are available. Although we used a behavioral model for simulations (i.e., an empirical base of telemetry locations to which we applied empirically derived rules of movement) to manually create a reference data set from which a probability distribution was generated, a better approach for future studies would be to write a model that specified the rules of movement. Thus, a computer-generated reference data set could be obtained which strictly adhered to rules set forth for the rate, and temporal and spatial patterns of movement (e.g., probability of locations occurring at latrine sites or within preferred habitat). Nonetheless, we believe that our manually created reference data set (Fig. A3.3) sufficiently emulated patterns of movement for coastal river otters (Figs. 1, 2, and 13) to permit assessment of the appropriate kernel method to use for estimates of linear home ranges.

The best method of home-range analysis should provide comparative information,

useful at the level of the population. An estimator that provides consistent information for an individual should permit greater confidence in the comparison of variability inherent among individuals in a population. Accordingly, our simulations represented a substantial amount of biological information pertaining to a single simulated individual as that individual traveled through its home range. Thus, for the purposes of estimating 95% linear home ranges, we sought to identify an analysis technique that provided relatively consistent results for simulations without requiring large numbers of locations.

Our results demonstrated that estimates of area (ha) overestimated true home-range area (Figs. 5a and 6a) for otters with movements associated with coastlines by including unused area in the estimates (Figs. 1c and 13). At first glance, figures 5a and 6a might lead to the conclusion that fx LSCV estimates of area were the best choice, but those data must be considered in concert with the variable smoothing for that technique and whether the area measured is representative of space use. In contrast to kernel methods with h_{ref} smoothing, in which estimates increased as number of locations increased, estimates with LSCV smoothing failed to show a consistent trend (Figs 5 and 6). Jones et al. (1996) also noted high variability with LSCV smoothing and "spurious bumps" indicating that such smoothing was unreliable. LSCV smoothing of our data often yielded numerous small, disjunct contours when locations were clumped (Fig. A3.1a), resulting in low area estimates. Depending on the distribution of clumped locations (compare Figs. 1 and 13), LSCV smoothing also resulted in contours and hence, home-range estimates equivalent to those with h_{ref} smoothing. Results from empirical data demonstrated that for many cases, LSCV smoothing could not reduce the error beyond

that of the reference smoothing parameter (h_{ref}), yielding equivalent estimates for both smoothing parameters (Table A3.3). Within a population, home-range estimates that resulted in numerous disjunct contours suggest an entirely different pattern of space use than for individuals for which LSCV did not result in fragmentation. That we noted such variation in home-range estimates (Fig.5) and fragmentation (Fig. A3.7) when sampling from the same simulated individual suggests that LSCV smoothing may not be appropriate for population-level comparisons for data with similar linear distributions. Differences in LSCV estimates might be attributable to the timing of sampling and perhaps a chance distribution of clumped data, or to inherent variability in the smoothing technique (Jones et al. 1996), rather than being representative of true differences in space use. Therefore, area estimates with fx LSCV methods appeared to be accurate (Figs. 5b and 6b) because high fragmentation (Fig. A3.7) resulted in underestimates of the true space use. By chance, those area estimates were numerically similar to "true" area. Fixed kernel LSCV estimates of area, however, are not a good method of estimating linear home ranges for coastal river otters because of inconsistencies in estimates with LSCV smoothing and because area not used by otters is included in the estimate (i.e., area not associated with shorelines).

Similarly, fx 0.8 did not appear to overestimate area compared with other kernel methods, however that also is misleading. By definition, fx 0.8 resulted in smaller estimates and more fractionation than fx h_{ref} estimates because it is a proportion of the bandwidth provided by fx h_{ref} estimates. Again, by numerical coincidence fx 0.8 area estimates were closer to "true" area due to smaller bandwidths, but area measurements

generally overestimated true area (Figs. 5b and 6b) by including unused area in the estimates (Figs. 1c and 13). Our shoreline estimates measured the km of shoreline within contours and provided a more accurate means of quantifying space use for species that use the aquatic-terrestrial interface (Figs 1,2, and 13). Therefore, we recommend that linear measures (e.g., km shoreline) should be used to estimate linear home ranges.

For 95% shoreline estimates for otters, we do not recommend LSCV smoothing because of inconsistencies in smoothing and because potentially spurious, disjunct contours may result in the exclusion of important foraging areas for coastal river otters that forage as they travel (Woolington 1984, Kruuk 1995). Regardless of smoothing parameter, kernel methods often converged upon h_{ref} estimates when LSCV smoothing could not further reduce error (Table A3.3). Similar studies are recommended to determine whether LSCV smoothing is appropriate for other species with linear patterns of movement. If LSCV smoothing provides more consistent results for other species, assessment of areas within disjunct contours may provide information about critical areas of use within the 95% home range.

Adaptive kernel estimates have been shown to overestimate home ranges compared with fixed kernel estimates (Seaman and Powell 1996). Larger estimates of km shoreline were obtained with adk h_{ref} methods and thus estimates that were closer to "true" shoreline length with fewer locations (Fig. A3.5a). Those estimates had greater variance (Fig. A3.5a), however, and were not remarkably different from those with fx h_{ref} methods (Fig. A3.6a). If all linear estimates are consistently underestimated (i.e., have less variance), comparisons among individuals within a population are likely to be more

meaningful. Therefore, we suggest that shoreline measurements within fx h_{ref} contours are more reliable estimates of linear home ranges because of greater consistency. The location of the modes are identified with fixed kernel estimates and h_{ref} smoothing (Jones et al. 1996), allowing for assessment of intense areas of use within a 95% home range, but oversmoothing and loss of fine details in the shape of a home range may occur (Worton 1995, Jones et al. 1996). The shape of the contour is of less concern, however, because the geographical feature that defines the linear movements is measured, rather than the area of the contour. Furthermore, an inspection of the contours produced from our simulations with fx h_{ref} estimates (data not shown) revealed that with 25 locations, the majority of locations occurred within the main bay but at least one, and often both of the excursive areas were identified. Although the total km shoreline in the home range was underestimated in our simulations with 25 locations, the general pattern of space use (i.e., main and excursive areas) generally was evident with only 1.7% of the possible reference data points (n = 1500, Fig. A3.3). Additionally, all home-range estimates for our empirical data and fx h_{ref} analyses approached an asymptote at $\bar{x}$ = 19.4 locations. Thus, results from our simulated and empirical data indicate that fx h_{ref} methods provide a reasonable estimate of space use with small numbers of locations.

A marked contrast between our results and those of several other studies of kernel estimators was the effect of small numbers of locations on estimates of home-range size. Differences in methodology to estimate utilization distributions (Fig. A3.8) cannot explain underestimates of home ranges in ours and other studies (de Solla et al. 1999 for subsamples from empirical data, Hansteen et al. 1999) compared with overestimates

(Worton 1995, Seaman and Powell 1996, de Solla et al. 1999 for simulations, and Seaman et al. 1999). Seaman et al. (1999) suggested that such discrepancies might be attributable to differences between the amount of smoothing provided by LSCV and h_{ref}, suggesting that LSCV increased smoothing and resulted in larger home ranges. We found that both smoothing parameters underestimated true home ranges (95% km shoreline) with small numbers of locations (Figs. 5a and 6a) and, commensurate with results reviewed by Jones et al. (1996), LSCV often resulted in undersmoothing and, for our data, smaller home ranges. Similar effects were reported by de Solla et al. (1999) that were attributable to the clumped distribution of their empirical data.

We offer alternative explanations for the directional differences in bias. One explanation may be the differences in spatial distribution of data points among the aforementioned studies. Whereas the authors reporting overestimates focused on simulations of movement patterns occurring anywhere within the simulated area, our simulations emulated otter movements confined to relatively linear pathways along coastlines. Similarly, de Solla et al. (1999) investigated antler flies (*Protopiophila litigata*) and snapping turtles (*Chelydra serpentina*), the latter of which confined movements to a shoreline, and Hansteen et al. (1999) examined data from three root voles that tended to use runways within their home ranges. It is possible that underestimation of home-range size with fewer locations is a phenomenon attributable to nonrandom movements, or perhaps linear patterns of space use. Alternatively, because we sampled our simulations in a chronological sequence, as did de Solla et al. (1999), our data often occurred in clumped distributions, some of which resulted in small bandwidths and

underestimates. Hansteen et al. (1999) resampled with replacement from their empirical data, a method also likely to result in a clumped distribution.

Finally, when comparisons between studies are considered, the discrepancies in estimates of home ranges may be due to differences in algorithms used by different home-range software packages. Larkin and Halkin (1994) and Lawson and Rodgers (1997) compared the output from several home-range analysis programs for a single data set and found considerable variation in the estimates produced. Larkin and Halkin (1994) reported that KERNEL HR produced a 95% adaptive kernel estimate with LSCV that was approximately twice as large as a 95% adk h_{ref} estimate for RANGES IV. Small numbers of locations resulted in bias in both directions, however, for de Solla et al. (1999) with KERNEL HR (Seaman and Powell 1991). Thus differences in software output is not the likely explanation for directional differences in bias between these studies, but variable results from different software are important to be aware of.

Core Areas (50% OD). – Whereas we promoted the use of an estimation technique that did not result in excessive fragmentation for assessing the exterior limits of a home range, we believe that important core areas that receive intensive use may not necessarily be contiguous. Analyses with h_{ref} smoothing generally produced only one contour, even with large sample size, and there was a significant negative relationship between number of contours and shoreline estimates (Table A3.2). In contrast, LSCV smoothing allowed for numerous contours, especially with more locations, and there was a subtle positive correlation between contours and shoreline estimates (Table A3.2). For fewer locations, the disparity in number of contours and shoreline estimates was minimal

among kernel methods (Fig. A3.9); thus all methods provided reasonable consistency in estimates when limited locations were available. Indeed, the difference in RMSE values among kernel methods was small for all numbers of locations (Fig. A3.10). Because fragmentation did not appear to substantially affect shoreline estimates of core areas with fx LSCV methods (Table A3.2) and may be useful for identification of critical areas within the core that may contain important resources, we recommend using fx LSCV to estimate km shoreline within core areas.

Autocorrelation

Just as our simulation and sampling methods offered a more realistic method of assessing the performance of home-range estimators, it also provided a more effective means of estimating the likelihood of collecting autocorrelated data in field studies and the effects of that autocorrelation on estimates of linear home ranges. McNay et al. (1994) found that even with a 6-week gap between locations, observations were not independent for 50% of 72 black-tailed deer (*Odocoileus hemionus columbianus*) because of seasonal migratory shifts or brief movements into previously unused areas within home ranges. There are many potential explanations for changes in sequential movement patterns for otters (e.g., a rich, ephemeral patch of prey that temporarily restricts movements for an otter until depleted). For our simulated data, we noted increasing positive autocorrelation with greater numbers of locations (Table A3.4) and our empirical data were often positively autocorrelated, even with few locations (Table A3.6). Thus we see that collection of data that are not autocorrelated presents a difficult challenge for animals with relatively linear distributions.

Swihart and Slade (1985*a*) suggested that independence is achieved when an animal's current position is not influenced by its position during past observations. We concur with de Solla et al. (1999) and Powell (2000); such independence is not biologically possible. Strong autocorrelation often results because animals typically move in a non-random fashion (Swihart and Slade 1985*a*, Legendre 1993, de Solla et al. 1999, Powell 2000). Once an animal has established a home range, the individual will have knowledge of features within the home range and will return repeatedly to important areas (e.g., foraging sites, or locations that provide shelter or other important resources), thus no location is biologically independent. Otis and White (1999) suggested that the sampling interval should be greater than the time required for the animal to traverse the home-range boundary. The interval at which data are collected may minimize the extent of autocorrelation in the data, but not all individuals in the population will use space at the same temporal or spatial scale. There are known differences in space use between sexes (Hansteen et al. 1999), and the range of t^2/r^2 values for our empirical data (Table A3.6) – differences that were not attributable to sex or age class – demonstrated that there was substantial variability in patterns of space use among individual otters.

We controlled for the confounding effects of sampling interval and number of locations, by keeping our sampling interval random. In contrast to most other studies, we simultaneously evaluated the effects of autocorrelation, number of locations, and kernel methods on home-range estimates with saturated-model MANOVAs (Tables 1 and 2). Although each kernel method responded differently when assessed collectively, when assessed individually, autocorrelation did not affect estimates of linear home ranges for

any of the kernel methods (Tables 1 and 2).

Our power to detect an effect of autocorrelation on shoreline estimates was relatively low (≤ 0.4), however, we did not detect the predicted relationship between home-range estimates and autocorrelation (Swihart and Slade 1985*b*): shoreline length did not decrease with increasing autocorrelation. In fact, for our simulated data we found the opposite trend, although that effect was not pronounced (Table A3.5). Similar to the results of de Solla et al. (1999), our simulations clearly demonstrated that as the number of locations increased, bias decreased (Figs. 5, 6, 9, and 10). Thus more locations provided a more accurate estimate of linear home ranges and, although autocorrelation increased with greater numbers of locations (Table A3.4), it had no apparent effect on linear estimates (Table A3.5). Also in agreement with de Solla et al. (1999) and their analyses of empirical data, we noted no relationship between t^2/r^2 and home-range size for our otter data (Table A3.3), even though extreme positive autocorrelation was noted in numerous cases (Table A3.6). Thus we presented considerable evidence that autocorrelation had no effect on kernel estimates of linear home ranges.

Schoener's ratio (t^2/r^2) can be effectively used to evaluate space use (Hansteen et al. 1999), because the non-independent phenomena represented in autocorrelated data may reveal important biological information (Legendre 1993, McNay et al. 1994, de Solla et al. 1999). Indeed, closer inspection of movement patterns for only two of our otters with high positive autocorrelation revealed significant behavioral details for both otters. The movements of the otter depicted in Fig. A3.1b (HB 25) were positively autocorrelated ($t^2/r^2 = 1.13$). Activities of this adult female suggested that she was denning (note the

cluster of three locations in the upper right hand corner with no movement between locations). Those observations occurred during a time consistent with initial denning and parturition for this species in marine environments in Alaska (Noll 1988). That cluster did not constitute a shift in home range (Swihart and Slade 1997), but did constitute a change in pattern of movements relative to home-range size (McNay et al. 1994) and resulted in autocorrelated data.

Consider the movement pattern for the otter with the greatest positive autocorrelation for a male otter (HB 26, Fig. A3.13b, $t^2/r^2 = 0.4$,). This adult briefly extended his range for the month of mating season (note the locations at the bottom of the figure), violating the assumptions of a stationary home range (Swihart and Slade 1997). Had we systematically eliminated those autocorrelated locations from our data set prior to analysis to control for the alleged effects of autocorrelation on estimates of home-range size, we would have lost critical information about reproductive strategies. An alternative approach might be to assess seasonal home ranges, but when few locations are available for an individual, extracting small subsets of those data may lead to an inability to assess home ranges or gross underestimates of home ranges with fewer locations (Figs. 5 and 9).

CONCLUSIONS

Our approach, using both simulated and empirical data, offers considerable insight into the effects of kernel methods, smoothing parameters, number of locations, and autocorrelation on determining home-range characteristics for species with relatively linear patterns of movement. Sampling from our simulations in a chronological sequence provided greater assurance that the performance of kernel methods was likely to be

applicable to empirical data, and results from our simulations closely matched that of our empirical data for 13 river otters. Whereas numerous studies have investigated analysis techniques for terrestrial mammals that use space with few restrictions, to our knowledge, this is the first study to investigate the best kernel method to use for analysis of linear patterns of space use that are common to many species. We used coastal river otters as our model, but any species that tends to restrict movements to a linear pathway associated with a geographical feature for which there is GIS coverage (e.g., creeks, rivers, altitudinal contours that represent valleys or ridgelines) can apply the techniques we presented. Some of these techniques also may be applicable to estimation of river length used by fish. While assessment of kernel methods for linear data was our main focus, we believe that many of our results can be applied to species that use space with less restriction. In particular, we recommend our method of simulations.

We recommend fixed kernel analyses with the reference smoothing parameter (h_{ref}) for linear estimates of 95% home ranges. We have shown that LSCV smoothing may result in the formation of numerous small disjunct contours for some configurations of clumped data (Figs. 1 and 13), leading to inconsistent results, and underestimates of linear home ranges. Such fragmentation may exclude important feeding areas for coastal river otters. If more consistent estimates with LSCV smoothing are obtained for other species with linear home ranges and there is some assurance that areas between disjunct contours have limited value (e.g., constitute poor habitat), those areas between contours may be considered as travel corridors and thus may not be as important to include in measures of home-range size. When issues of habitat conservation are considered, however, some

estimate of likely area for such travel corridors should be included. Similarly, for linear estimates, an animal will not always be found exactly on the geographical feature that defines the linear movements (Figs. 1, 2, and 15). Thus if there is a need for finer scale measurements for linear estimates, a buffer zone can be incorporated around the linear feature within the limits of the contour(s). The size of the buffer would be species and habitat dependent, but should be wide enough to encompass a reasonable distance away from the geographical feature in which the animal might be expected to be located (e.g., mean distance from shore, or mean plus 1 or 2 standard deviations).

We demonstrated that autocorrelation had no apparent effect on linear estimates of home ranges with any kernel method for our simulated and our empirical data. Moreover, our empirical data clearly demonstrated that patterns of space use associated with autocorrelation may provide insight into important behavioral information. We concur with Legendre (1993), McNay et al. (1994), de Solla et al. (1999) and Hansteen et al. (1999) – tests for independence among data should be viewed as a tool to evaluate space use rather than an obstacle to home-range analyses.

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Table A3.1. A comparison among kernel methods of the effects of increasing numbers of locations (n) and autocorrelation (t^2/r^2) on estimates of shoreline length (km) and numbers of contours for 95% home ranges.

Kernel Method		Model (P; MANOVA)	n	Homogenous subsets †for n	t^2/r^2	t^2/r^2 * n	Corr ‡ P (r)
adk LSCV	Shore	< 0.001	0.6		0.2	0.9	< 0.001
	Contour #	< 0.001	0.6		0.5	0.9	(-0.44)
adk h_{ref}	Shore	< 0.001	< 0.001	25=50=100=1500 50=100=200=1500	0.2	0.04	< 0.001
	Contour #	0.03	0.3		0.2	0.4	(-0.19)
fx LSCV	Shore	< 0.001	0.04	25=50,100=200	0.6	0.1	0.9
	Contour #	< 0.001	0.2		0.8	0.3	(-0.007)
fx h_{ref}	Shore	< 0.001	< 0.001	25=50, 50=100, 100=200=1500	0.1	0.06	< 0.001
	Contour #	< 0.001	0.9		0.5	0.9	(0.17)
fx 0.8	Shore	< 0.001	< 0.001	25=50, 100=200, 200=1500	0.2	0.2	< 0.001
	Contour #	< 0.001	0.04	15=25=50, 100=200	0.4	0.04	(0.19)
All Kernel methods ◊	Shore	< 0.001	< 0.001	25=50, 50=100, 50=100=200	0.01	0.05	< 0.001
	Contour #	< 0.001	0.2		0.6	0.4	(-0.27)

† Post-hoc Scheffe multiple comparisons among sample sizes ($P > 0.05$; MANOVA), LSCV smoothing could not be assessed for n=1500, contour numbers were not assessed for n=1500.

‡ Correlation (Pearson) between estimates of shoreline length and number of contours.

◊ P values are for overall model and for effects of kernel method on estimates of shoreline and contours. Estimates of km shoreline were similar between fx h_{ref} and adk LSCV (P = 0.9, MANOVA post-hoc Scheffe).

Table A3.2. A comparison among kernel methods of the effects of increasing numbers of locations (n) and autocorrelation (t^2/r^2) on estimates of shoreline length (km) and numbers of contours for 50% core home ranges.

Kernel Method		Model (P; MANOVA)	n	Homogenous subsets for n	t^2/r^2	$t^2/r^2 * n$	Corr † P (r)
adk LSCV	Shore	< 0.001	0.02	none	0.2	0.6	< 0.001
	Contour #	< 0.001	0.6		0.6	0.9	(-0.44)
adk h_{ref}	Shore	< 0.001	< 0.001	none	0.4	0.5	0.003
	Contour #	< 0.001	0.6		1.0	1.0	(-0.13)
fx LSCV	Shore	< 0.001	0.002	25=50, 100=200	0.5	0.04	< 0.001 (0.16)
	Contour #	< 0.001	0.07		0.8	0.4	
fx h_{ref}	Shore	< 0.001	< 0.001	100=200	0.3	0.3	< 0.001
	Contour #	< 0.001	0.6		0.7	0.7	(-0.38)
All Kernel methods	Shore	< 0.001	< 0.001	none	0.05	0.5	0.001
	Contour #	< 0.001	0.05	15=25=50	0.5	0.01	(-0.08)

† Correlation (Pearson) between estimates of shoreline length and number of contours.

Table A3.3. A comparison of 95% shoreline estimates (km) among kernel methods for empirical data collected from river otters radiotracked in Herring Bay, Prince William Sound, Alaska, in 1998.

OTTER	adk LSCV	adk h_{ref}	fx LSCV	fx h_{ref}	fx 0.8	adkh_{ref} - fxh_{ref}*
HB06	38.1	38.1	30.3	30.3	25.9	7.8
HB08	20.1	20.1	19.4	19.4	16.1	0.7
HB09	21.1	21.1	20.4	20.4	20	0.7
HB21	12.9	12.9	12.2	12.2	12.4	0.7
HB22	13.4	40.7	12.0	34.9	30.6	5.8
HB23	5.4	13.8	3.6	10.1	8.6	3.7
HB25	2.4	9.8	2.1	8.9	7.6	0.9
HB26	50.8	50.8	47.2	47.2	38.8	3.6
HB32	11.1	52.1	11.5	40.5	34.9	11.6
HB33	2.3	10.3	2.1	9.7	9.1	0.6
HB34	15.3	15.3	14	14.0	13.4	1.3
HB35	6.9	15.6	7.3	15.5	15.3	0.1
HB36	7.9	13.5	5.4	11.7	9.7	1.8
Shore/t^2/r^2						
P (*r*) †	0.9 (0.05)	0.7 (0.13)	0.9 (-0.03)	0.8 (0.08)	0.7 (0.12)	

* MSE was similar between these 2 kernel methods for simulations.

† Correlation (Pearson two-tailed) between shoreline estimates and autocorrelation (t^2/r^2). Results from a saturated model MANOVA ($P = 0.5$) comparing shoreline estimates among kernel methods, corrected for sex differences, were as follows: kernel method $P = 0.5$, power ($\alpha = 0.5$) = 0.25; autocorrelation (t^2/r^2) $P = 0.9$, power = 0.05; number of locations (*n*) $P = 0.3$, power = 0.16; sex $P = 0.04$, power 0.53; method * t^2/r^2 $P = 0.8$ power = 0.14; method * *n*

$P = 0.5$, power = 0.24; t^2/r^2* *n* $P = 0.9$, power = 0.05; method * t^2/r^2 * *n* $P = 0.8$, power = 0.12.

Table A3.4. Schoener's ratio (t^2/r^2) values for simulations (n = 100 replicates for each set of numbers of locations). Decreasing values of t^2/r^2 reflect increasing positive autocorrelation.

Number of locations	15	25	50	100	200
$\bar{x}$	1.94	1.93	1.84	1.52	0.93
95% Confidence Interval	1.13 - 2.76	1.33 - 2.53	1.43 - 2.26	1.27 - 1.76	0.81 - 1.05
$t^2/r^2 \leq 2$ (n)	56	56	75	100	100
$t^2/r^2 \leq 1.5$ (n)	13	9	9	46	100

Table A3.5. Analysis of the relationship between Schoener's Ratio (t^2/r^2) for simulations and linear estimates of home ranges (two-tailed Pearson correlation). Increases in positive autocorrelation are indicated by decreasing values of t^2/r^2.

Number of locations	adk LSCV *P* (*r*)	adk h_{ref} *P* (*r*)	fx LSCV *P* (*r*)	fx h_{ref} *P* (*r*)	fx 0.8 *P* (*r*)
15	0.3 (-0.11)	0.5 (0.07)	0.8 (-0.03)	0.5 (0.06)	0.8 (0.03)
25	0.02 (-0.24)*	0.01 (-0.25)*	0.2 (0.13)	0.03 (-0.22)*	0.05 (-0.20)*
50	0.3 (-0.10)	0.2 (-0.15)	0.04 (-0.21)*	0.4 (-0.08)	0.4 (-0.09)
100	0.7 (-0.04)	0.6 (-0.06)	0.7 (0.04)	0.6 (0.06)	0.6 (0.06)
200	0.9 (0.003)	0.2 (-0.13)	0.5 (-0.08)	0.01 (-0.28)*	0.05(-0.20)*

* Indicates significant correlations.

Table A3.6. Schoener's ratio (t^2/r^2) values for river otters radio-tracked in Herring Bay, Prince William Sound, Alaska, in 1998.

Otter	**HB06**	**HB08**	**HB09**	**HB21**	**HB22**	**HB23**	**HB25**	**HB26**	**HB32**	**HB33**	**HB34**	**HB35**	**HB36**
Sex*	male	male	male	female	male	male	female	male	male	male	male	female	male
Age †	adult	adult	adult	adult	yrlng	yrlng	adult	adult	adult	yrlng	yrlng	yrlng	yrlng
t^2/r^2 ‡‡	2.24	1.5	2.22	0.21	1.17	1.61	1.13	0.4	1.78	0.34	1.8	2.09	0.62

* There was no difference between males and females in the level of autocorrelation ($P = 0.98$), between age classes ($P = 0.37$), and the interaction was not significant ($P = 0.07$) with two-way analysis of variance.

† yrlng = yearling

‡‡ t^2/r^2 $\bar{x} = 1.32$, SE = 0.2

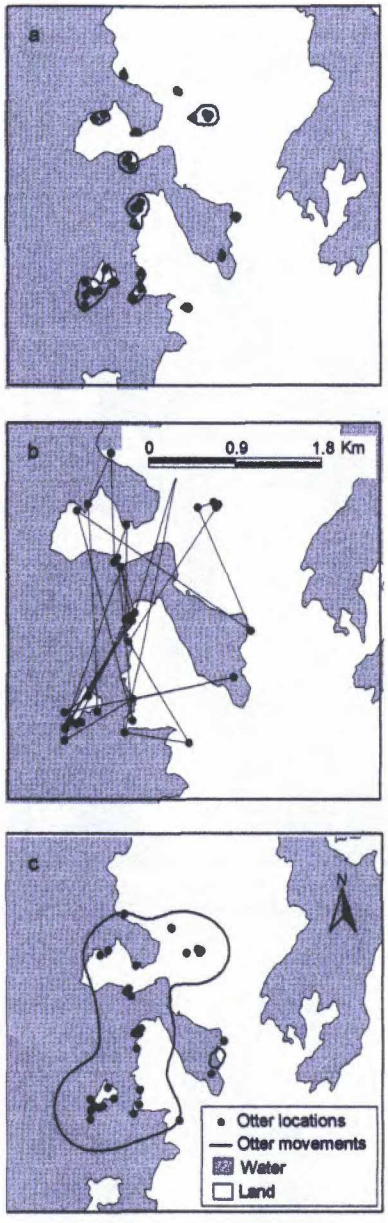

Figure A3.1 - Fixed kernel estimates of the 95% home range for an adult female river otter (HB 25) in Herring Bay, Prince William Sound, Alaska, in 1998 (n = 32 locations). Fixed kernel contours with least squares cross validation (**a**). The lines (**b**) demonstrate the chronological sequence of locations, not the actual route taken. Fixed kernel contour with the reference (h_{ref}) smoothing parameter (**c**). Locations were positively autocorrelated ($t^2/r^2 = 1.13$).

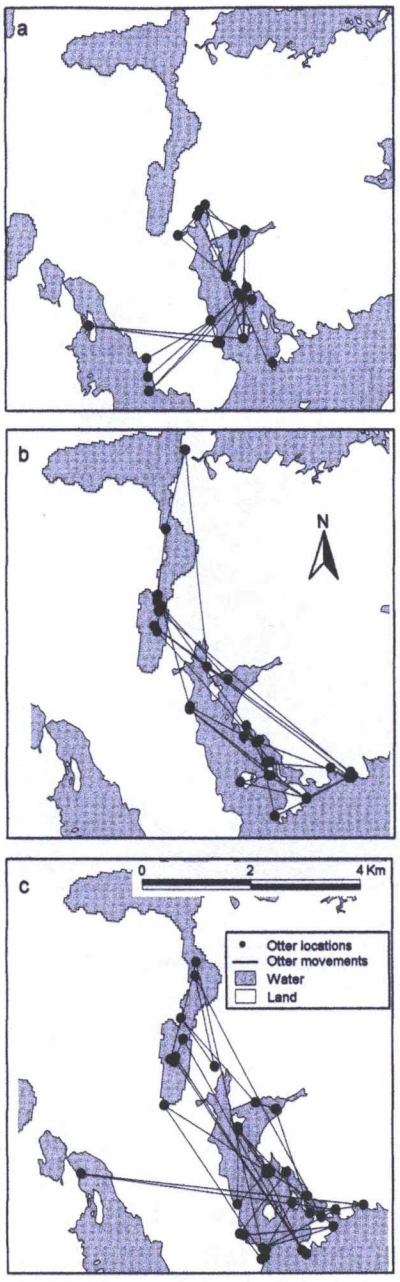

Figure A3.2 - Three years of telemetry locations obtained for an adult male river otter (JP11) in Dangerous Passage, 60 ° 20'N, 148 ° 10'W, Prince William Sound, Alaska from 1996-1998. In 1996 (**a**), locations were obtained an average of 56.7 hours apart. Sampling intervals for 1997 (**b**) were $\bar{x}$ = 13.1 days, and for 1998 (**c**) $\bar{x}$ = 9.9 days. Movements were comparable between years: ≥ 71% of locations in each year occurred in a single bay and distance between successive locations were similar (see methods), suggesting a similar pattern of space use for short and long-term movements. Lines indicate the chronological sequence of locations.

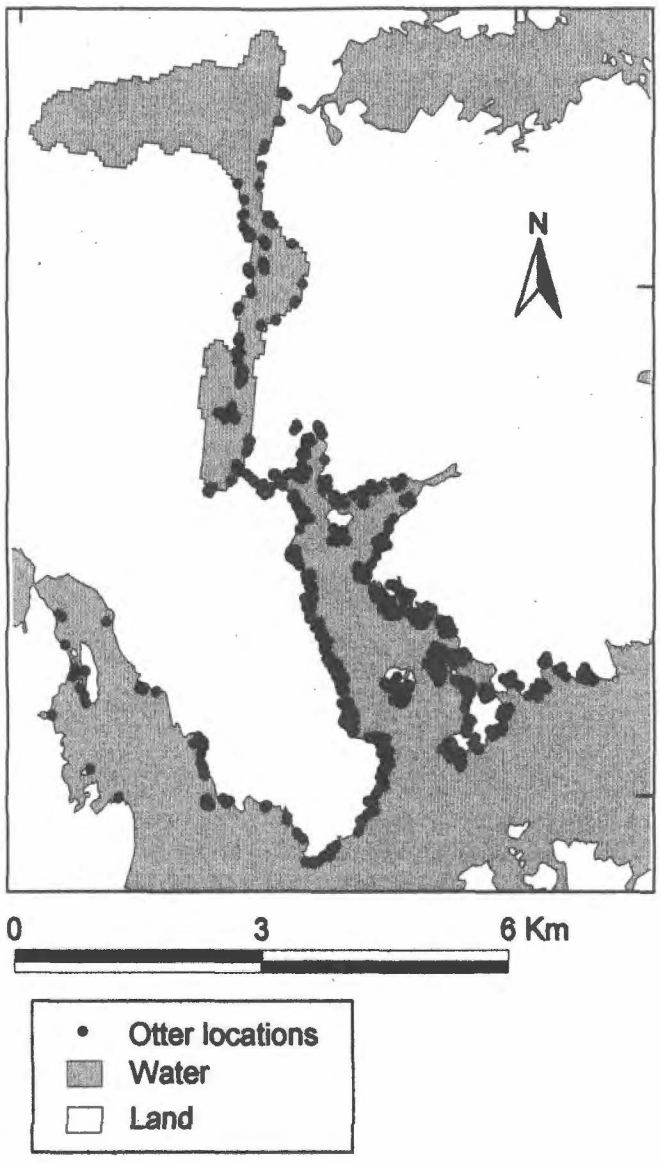

Figure A3.3 - Reference locations used to generate a utilization distribution. Locations (n = 1500) were based upon data from JP11 (Figure A3.2) and a behavioral model. See methods for details.

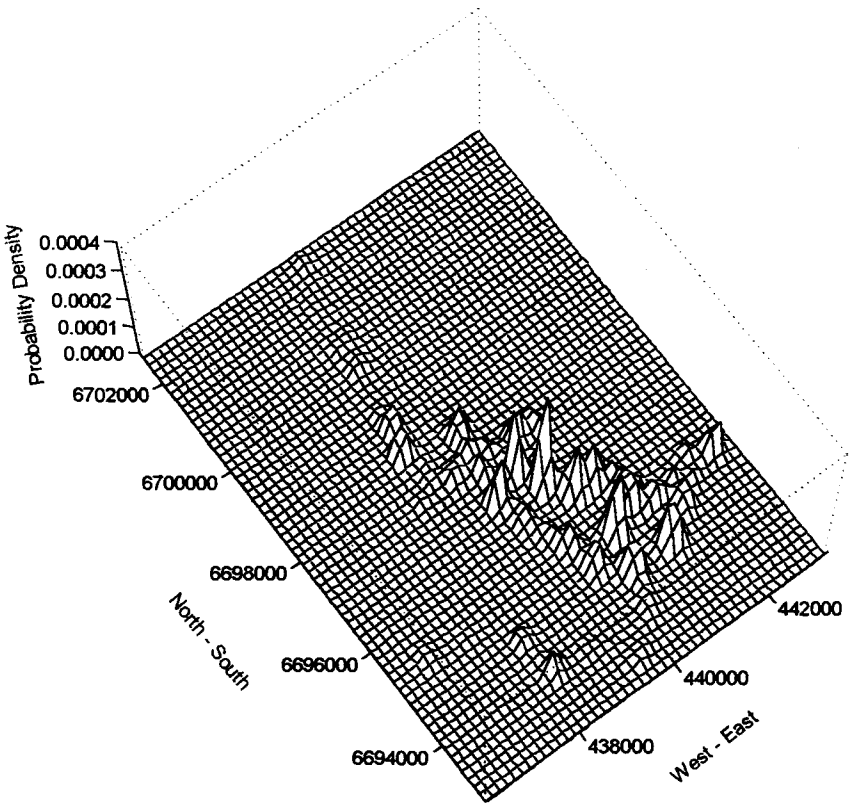

Figure A3.4 - Utilization distribution created to simulate otter movements in Prince William Sound, Alaska. Locations in the reference data set (Figure A3.3) served as the centers of 1500 bivariate normal distributions, which were used to create the probability distribution. Larger values on the vertical axis represents areas with a greater probability of use.

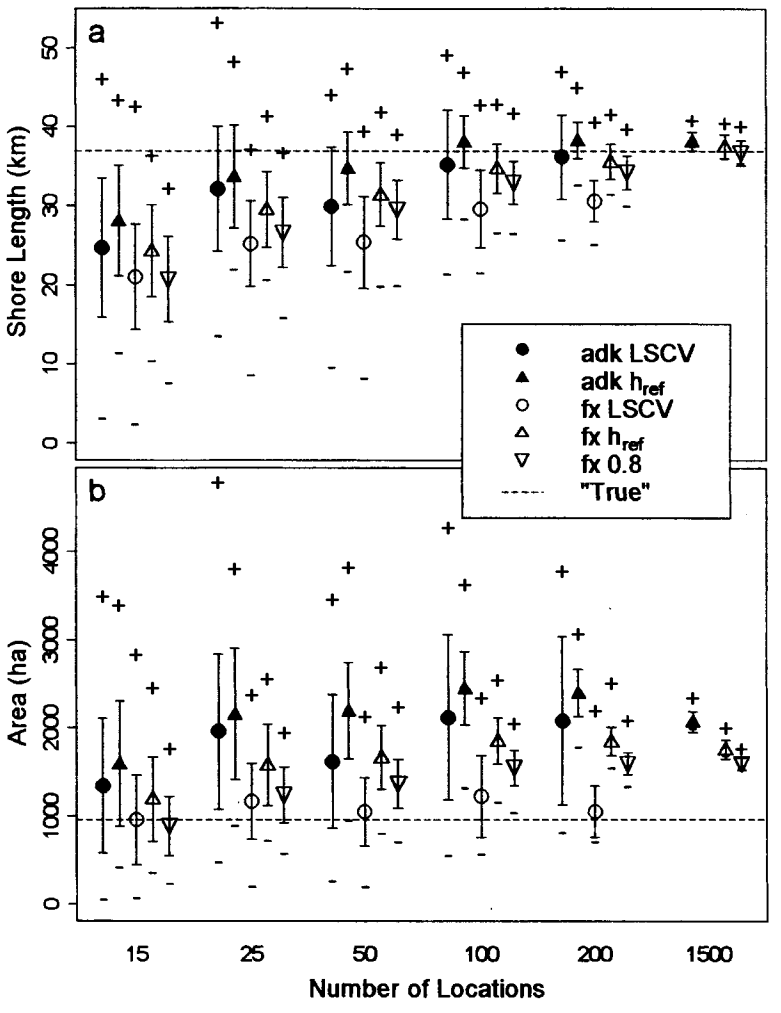

Figure A3.5 - A comparison of 95% home-range estimates for each kernel method for km shoreline (**a**), and area (**b**) with increasing numbers of locations. "True" represents the 95% probability distribution for shoreline (**a**) and area (**b**), calculated from the simulated utilization distribution (Fig. 4). Symbols are mean values, error bars are 1 SE, + and – symbols are maximum and minimum estimates, respectively. Adk = adaptive kernel, fx = fixed kernel, LSCV = least squares cross validation, h_{ref} = reference smoothing parameter.

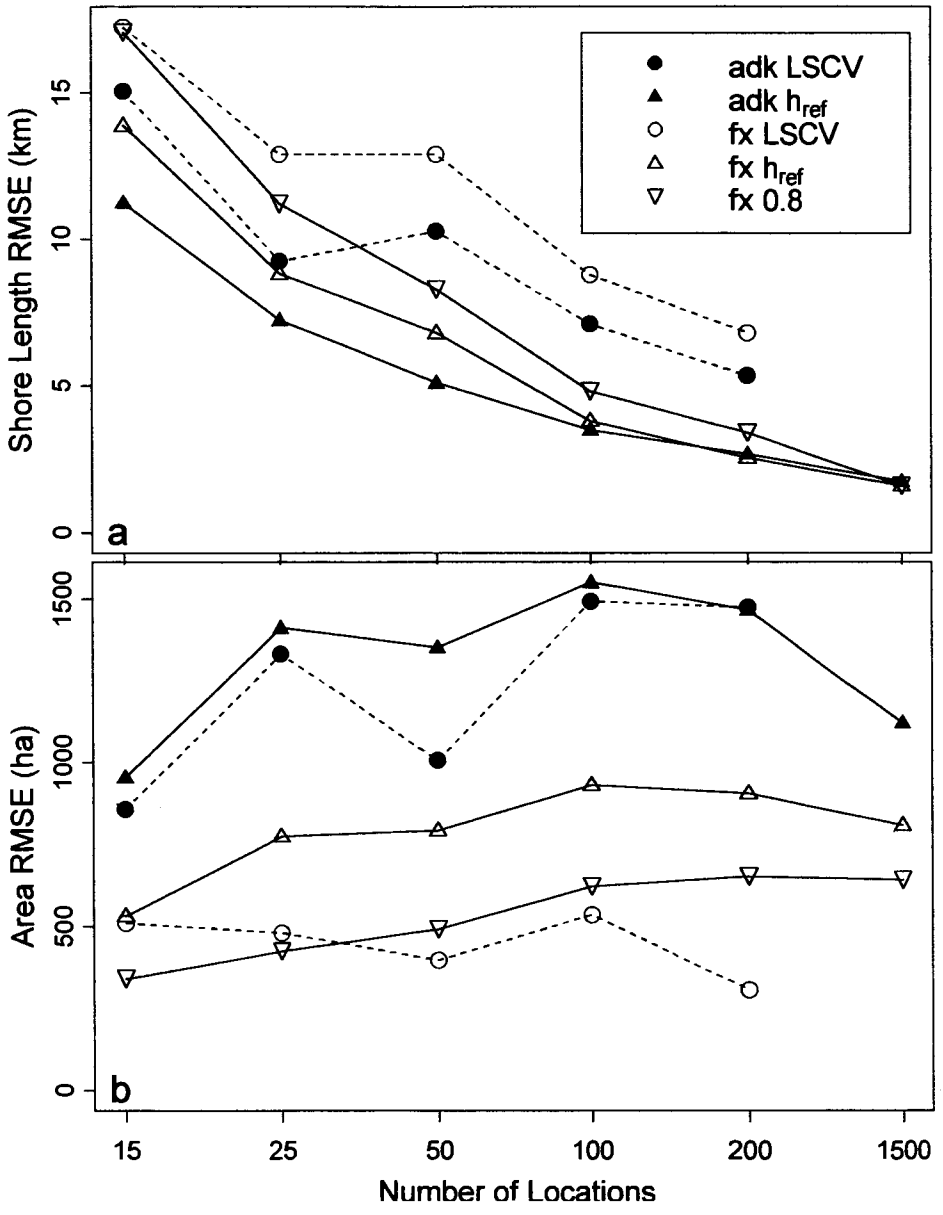

Figure A3.6 - A comparison of the root mean squared error (RMSE) among kernel methods for 95% km shoreline (**a**) and area estimates (**b**). Lines do not indicate a continuous variable: dashed lines demonstrate trends with LSCV smoothing and solid lines indicate trends with h_{ref} smoothing.

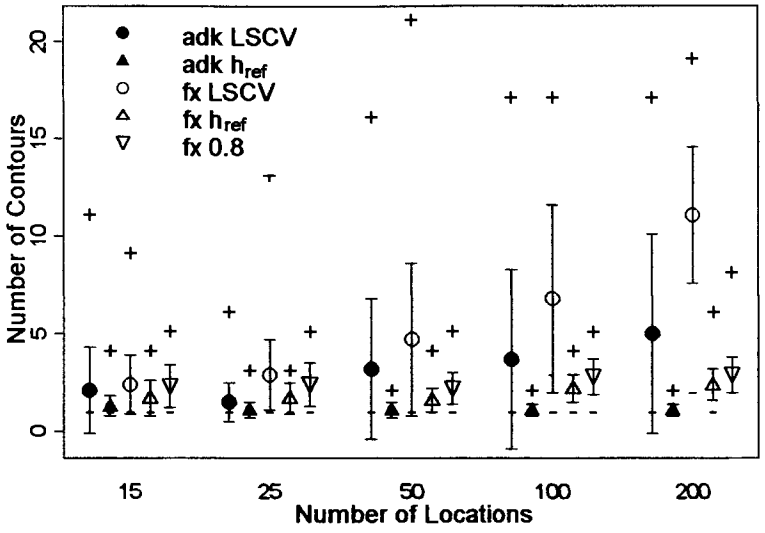

Figure A3.7 - Mean number of contours produced with each kernel method for 95% home-range estimates. Symbols, error bars, and abbreviations are defined in Figure A3.5. Number of contours differed among methods of kernel estimates ($P > 0.5$ MANOVA post-hoc Scheffe), and contour number showed a significant effect of number of locations only for fx 0.8 (Table A3.1).

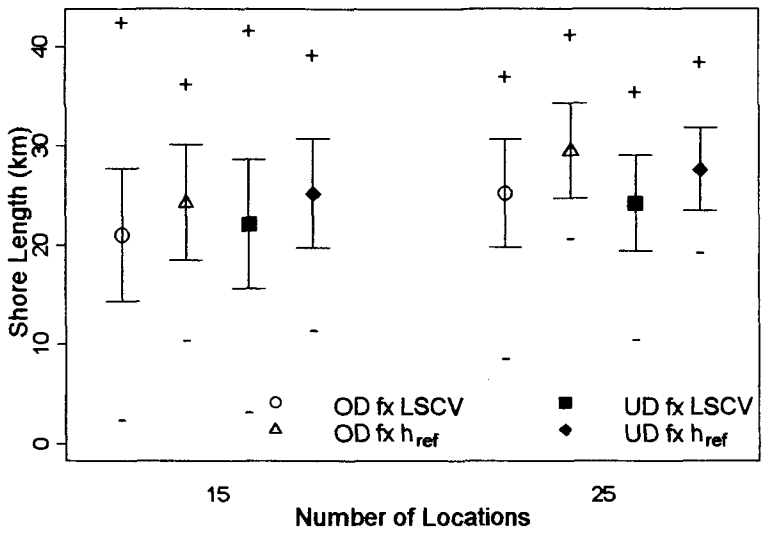

Figure A3.8 - A comparison of 95% shoreline estimates based on the utilization distribution obtained from a percentage of locations (i.e., the observation density – OD) and estimates based on the volume of the utilization distribution (UD) for fixed kernel methods with LSCV and reference (h_{ref}) smoothing. Symbols, error bars, and abbreviations are defined in Figure A3.5. There was no difference between OD and UD estimates for fx LSCV ($P = 0.9$, MANOVA) or fx h_{ref} ($P = 0.4$) estimates, but number of locations was significant for both techniques (OD vs. UD, $P < 0.001$). The interaction between n and technique was significant for fx h_{ref} ($P = 0.008$) but not for fx LSCV ($P = 0.06$ MANOVA).

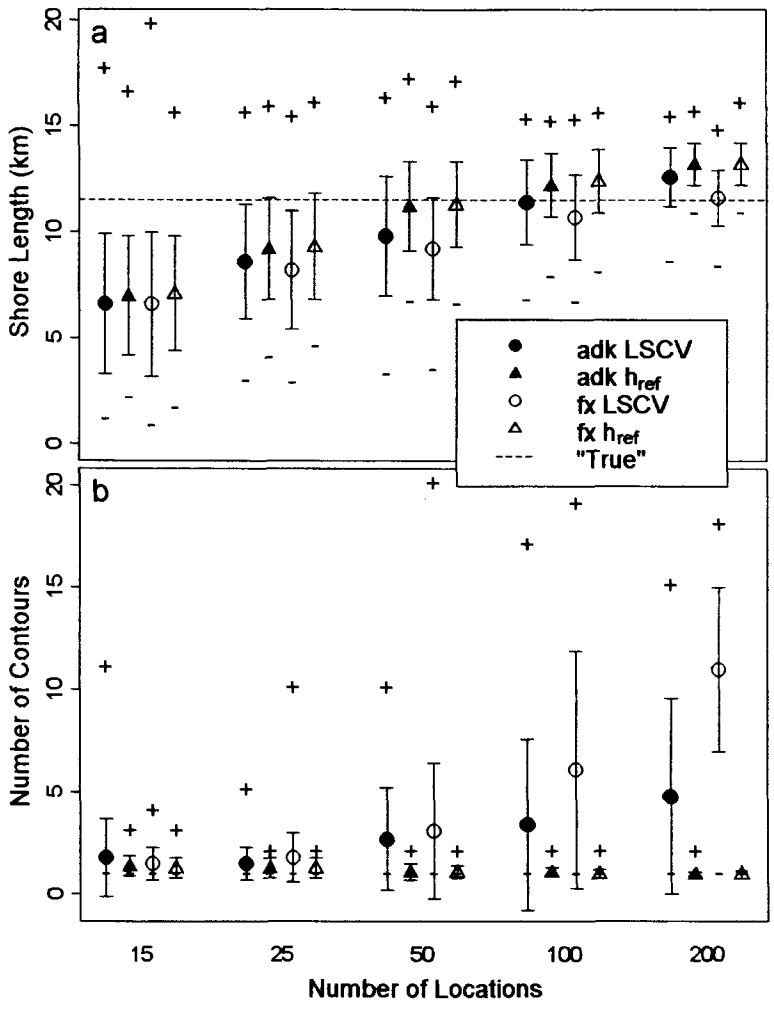

Figure A3.9 - A comparison of 50% core home ranges among kernel methods with increasing numbers of locations for estimates of km shoreline (**a**) and numbers of contours (**b**). Symbols, error bars, and abbreviations are defined in Figure A3.5. Shoreline estimates and number of contours were similar for adk h_{ref} and fx h_{ref} analyses ($P = 0.9$, MANOVA post-hoc Scheffe).

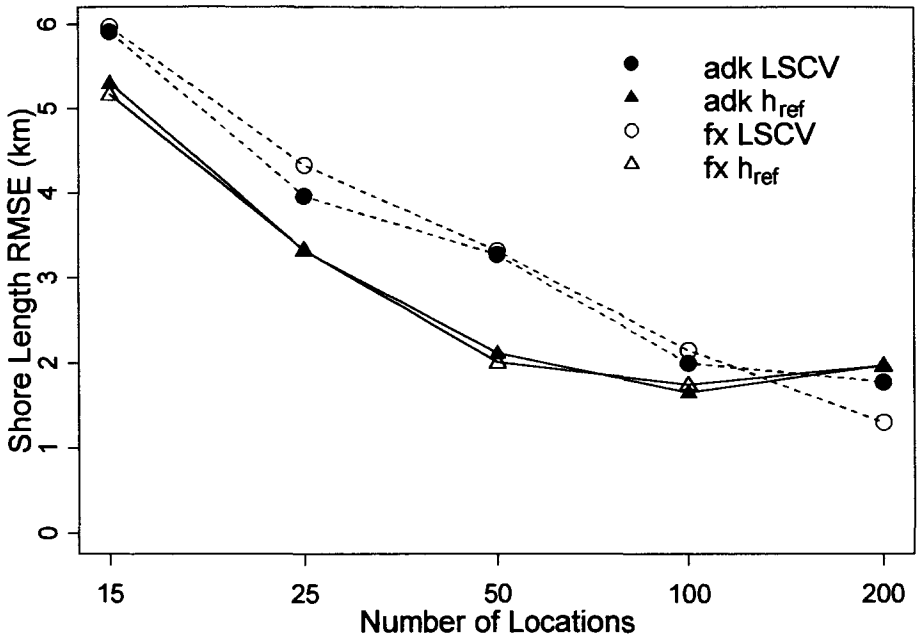

Figure A3.10 - A comparison of the root mean squared error (RMSE) among kernel methods for 50% core estimates of km shoreline. Lines do not indicate a continuous variable: dashed lines demonstrate trends with LSCV smoothing and solid lines indicate trends with h_{ref} smoothing.

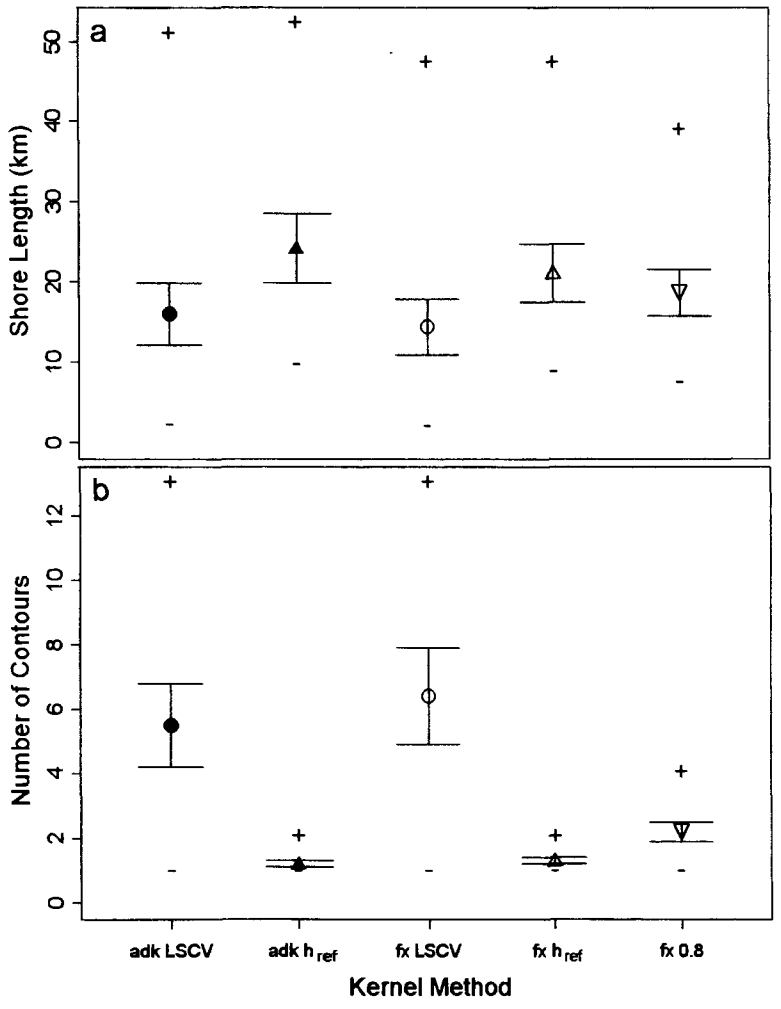

Figure A3.11 - A comparison of km shoreline estimates (**a**) and number of contours (**b**) among kernel methods for 95% home ranges for river otters (n = 13) in Herring Bay, Prince William Sound, Alaska, in 1998. Symbols, error bars, and abbreviations are defined in Fig. 5. Shoreline estimates did not differ among kernel methods (see Table 3) and contour numbers were similar for all h_{ref} methods (P = 0.95) and for LSCV methods (P = 1.0, MANOVA post-hoc Scheffe).

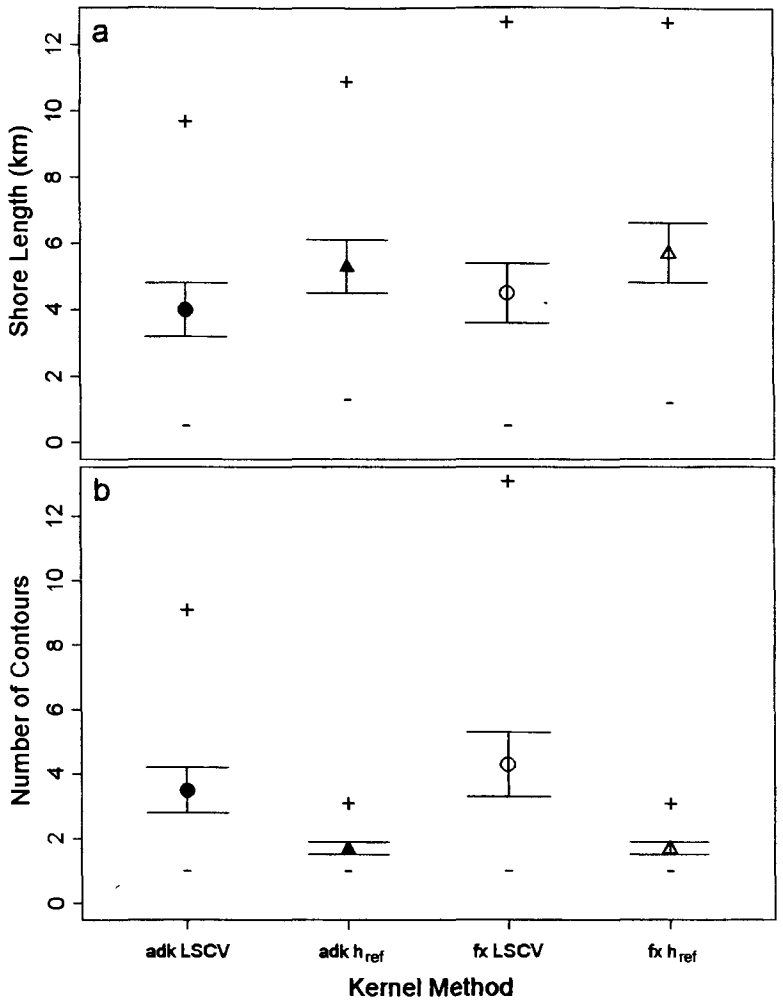

Figure A3.12 - A comparison of km shoreline estimates (**a**) and number of contours (**b**) among kernel methods for 50% core areas for river otters (n = 13) in Herring Bay, Prince William Sound, Alaska, in 1998. Symbols, error bars, and abbreviations are defined in Figure A3.5. Shoreline estimates were similar among adk LSCV, fx LSCV, and adk h_{ref} methods (P = 0.06), and among fx LSCV, adk h_{ref} , and fx h_{ref} methods (P = 0.08, MANOVA post-hoc Scheffe). Number of contours was similar among estimates with h_{ref} smoothing (P = 0.99) and between estimates with LSCV smoothing (P = 1.0, MANOVA post-hoc Scheffe).

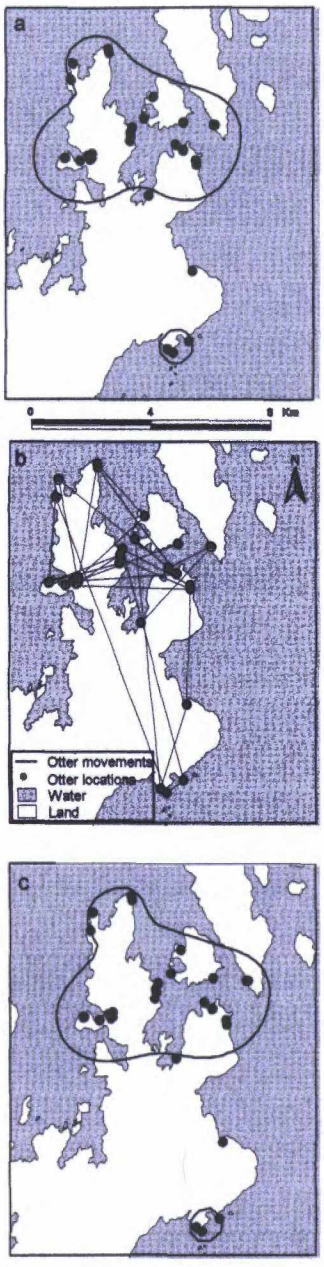

Figure A3.13 - Kernel methods used to estimate 95% km shoreline for an adult male river otter (HB 26) in Herring Bay, 60 ° 30'N, 147 ° 40'W, Prince William Sound, Alaska, in 1998 (n = 30 locations). Adaptive kernel contour with LSCV smoothing (**a**). The lines (**b**) demonstrate the chronological sequence of locations, not the actual path taken by the otter. Fixed kernel contour with h_{ref} smoothing (**c**). Note the similarity in contours between LSCV and h_{ref} smoothing for this otter compared with Fig. 1 where a different pattern of clumped data led to fragmentation with LSCV smoothing. These locations were positively autocorrelated ($t^2/r^2 = 0.04$). The extension of home range (note locations at bottom of figure) represents a temporary range expansion associated with the month of mating season (May).